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The Utility of Light-Saturation Models for Estimating Marine Primary Productivity in the Field: A Comparison with Conventional "Simulated" In Situ Methods

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Primary production rates derived from model photosynthesis–light (P–I) curves and daily solar radiation data were compared with direct measurements using "simulated" in situ incubations in arctic and temperate marine waters. On the average, model estimates were slightly higher in surface waters and significantly lower at the bottom of the euphotic zone (1% light level) than were the measured values. This could be partially explained by spectral differences in incubation light sources. However, areal production rates were statistically indistinguishable. Use of P–I models without a photoinhibition term and incorporating P–I pararmeters from mixed-layer populations gave the best overall agreement with directly measured production rates.

Les auteurs comparent les taux de production primaire dérivés de courbes-modèles de la photosynthèse en fonction du flux lumineux (P–FL) et de données sur le rayonnement solaire quotidien aux quantifications directes, à l'aide d'incubation *in situ* simulées dans les eaux marines arctiques et tempérées. En moyenne, les estimations-modèles étaient légèrement plus élevées dans les eaux superficielles et nettement plus faibles dans la partie inférieure de la zone euphotique (taux de luminosité : 1 %) que les valeurs quantifiées. Les différences spectrales entre les sources lumineuses utilisées pour l'incubation peuvent expliquer en partie ces différences. Toutefois, les taux de production superficielle étaient statistiquement indiscernables. L'utilisation de modèles P–FL sans valeur de photoinhibition et regroupant des paramètres P–FL relatifs aux populations occupant la couche mixte a fourni le meilleur accord global avec les taux de production directement quantifiés.

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Field techniques for measuring primary production with the ^{14}C method have varied considerably since its earliest application in the marine environment (Steemann-Nielsen 1952). Diversity in methodology has been a source of difficulty in intercomparisons of values from different studies for larger scale (regional to global) estimates of primary productivity (e.g. Platt and Subba Rao 1975). With the exception of minor variations, three basic experimental designs have been used (Strickland 1965; Finenko 1978). The most universally accepted is the in situ (IS) method, in which samples are incubated in their natural environment. Whereas this is probably the most reliable and realistic method of incubation, it has limited practical applicability for sea-going survey operations.

An alternative is the "simulated" in situ (SIS) method; samples are incubated aboard ship in deck boxes which are light-attenuated to simulate their natural light environment and temperature-regulated by flowing seawater. Results using this technique have compared favorably with IS results (Berge 1958; Jitts 1963; Doty et al. 1965; Jitts et al. 1976; Head 1976; Brown 1982) and the SIS method probably remains the most widely used in marine primary production studies.

A more recently introduced calculative (or model) method involves computation of productivity using measured solar radiation data, attenuation coefficients, and a mathematical description of the relationship between photosynthesis and light (P–I curve) determined empirically for the natural phytoplankton population. Early attempts at estimating primary productivity using very simple models were of limited utility (e.g. Ryther 1956; Ryther and Yentsch 1957). More recent studies employing better established P–I relationships have generally shown close agreement between model, IS, and SIS estimates of primary production rate (Fee 1973a, 1973b; Jitts et al. 1976; Gargas and Nielsen 1976; Colijn et al. 1983; Côté and Platt 1984). However, these intercomparison studies have most often been restricted to a specific geographic location, depth stratum, or time of year and have not established the larger scale (temporal or spatial) and more general utility of this method. The model method has clear logistical advantages over conventional SIS or IS methods when high-resolution (in space or time) data on primary production are required (Fee 1973a, 1973b; Jitts et al. 1976). Moreover, the potential value of this approach is most evident now when considering recent advances in in situ biological profiling instrumentation (e.g. Herman and Denman 1976; Herman et al. 1984) and in modelling the photosynthesis–light (P–I) relationship (e.g. Platt et al. 1977; Platt and Gallegos 1980; Gallegos and Platt 1981).

For a number of years our primary production studies, encompassing a variety of marine environments, have included both conventional SIS measurements of water column production and high-precision analyses of P–I relationships. Only recently, however, have we employed our P–I data to estimate water column production rates (Herman and Platt 1983; Herman 1983; Platt and Herman 1983; Herman 1984; Herman and Platt 1985). Here, we summarize the results of a comparison of the SIS and model methods from three cruises in arctic and temperate waters with emphasis on the effects of depth variations in P–I parameters and of the selection of P–I models on water column production estimates.

Methods

Primary production measurements were made on three cruises, two to the eastern Canadian Arctic and one on the continental shelf off Nova Scotia. Twelve stations were occupied during the 1978 cruise to the Arctic (ARC 78), covering an area from 62 to 78°N, and from 26 August to 14 September (Irwin et al. 1980). Eleven stations were occupied subsequently in the same general area (ARC 80) during the period 24 July – 28 August 1980 (Irwin et al. 1983a). Eight stations were sampled on the Scotian Shelf (SLF 79) from 18 April to 2 May 1979 in the area surrounding 43°N, 62°W (Irwin et al. 1983b).

Water samples were collected using 30-L Niskin bottles from five depths (based on Secchi disc lowerings) corresponding to 100, 50, 25, 10, and 1% light penetration. SIS productivity measurements and chlorophyll *a* (Holm-Hansen et al. 1965) were determined for each depth. P–I measurements were typically made at two depths (50 and 1% light levels). Because of the highly stratified nature of the water column in all three cruises (see Platt et al. 1982), samples from the 50% light level invariably represented phytoplankton populations from the upper mixed layer, while 1% light level populations were most frequently associated with the subsurface chlorophyll maximum layer. Samples were usually collected in the morning. Incident solar radiation was measured by taking hourly averages from a LICOR® LI-200S pyranometer sensor coupled to a recording integrator (LICOR L1550). Photosynthetically active radiation (PAR) was taken as 45% of the pyranometer value.

For the SIS experiments, ~200-mL seawater samples were inoculated with $H^{14}CO_3^-$ (185–370 kBq) and incubated in deck boxes attenuated with neutral density nickel screens (Perforated Products, Brookline, MA) for 24 h under natural sunlight conditions (Harrison et al. 1982). Temperature was controlled with flowing surface seawater. Precision of replicate determinations averaged ±10–15%.

P–I experiments used in the determination of model parameters involved the incubation of 30–50, 100-mL samples with $H^{14}CO_3^-$ (185–370 kBq) for 2–4 h in an unfiltered artificial light gradient (Platt et al. 1980). All incubations were terminated by filtration of samples through glass fiber filters (Whatman GF/F). Filters were rinsed with seawater and analyzed later by scintillation spectrometry. "Time-zero" or "dark-bottle" determinations served as blanks.

Results from light-gradient incubations were used to construct two model P–I curves for each experiment. One describes the dependence of photosynthesis on light, up to light-saturation, and employs a hyperbolic tangent (HT) equation (Jassby and Platt 1976):

$$(1)\quad P^B = P_m^B \cdot \tanh \cdot (\alpha I / P_m^B)$$

TABLE 1. Precision of P–I model parameter estimates. Mean relative error = 90% confidence interval/2·parameter estimate.

Cruise	No. of observations	Mean relative error (±%)		
		P_s	α	β
ARC 78	24	16	21	43
ARC 80	16	7	11	23
SLF 79	16	8	6	20

where P^B is the production normalized to chlorophyll *a* biomass (mg C·mg $Chl^{-1}\cdot h^{-1}$), P_m^B is the maximum rate at light saturation (same units as P^B), α is the initial slope of the P–I curve (mg C·mg $Chl^{-1}\cdot h^{-1}\cdot W\cdot m^{-2}$), and I is the light level ($W\cdot m^{-2}$, PAR). The other curve describes the P–I response including supraoptimal (photoinhibiting) light levels and employs an exponential (E) equation (Platt et al. 1980):

$$(2)\quad P^B = P_s^B \cdot (1 - e^{-\alpha I/P_s^B}) \cdot e^{-\beta I/P_s^B}$$

where P_s^B is a scaling parameter representing the maximum *potential* rate if there were no photoinhibition (same units as P_m^B) and β characterizes the negative slope of the curve at high light levels (same units as α). P_m^B (eq. 1) and P_s^B (eq. 2) are equivalent when $\beta = 0$. Both models were found to be good empirical representations of the diversity of experimental results we have collected to date. Precision of parameter estimates is given in Table 1; techniques used to estimate confidence regions are described in Irwin et al. (1980).

Absolute hourly primary production rates ($P(t)$) over an experimental day were in turn computed from P–I curves, hourly PAR values ($I(t)$), and phytoplankton biomass data:

$$(3)\quad P(t) = P^B(I(t)) \cdot B.$$

Rates for each light depth were computed using 100, 50, 25, 10, and 1% surface light values. Daily rates were then calculated by summing hourly rates:

$$(4)\quad P_v = \sum_{t=1}^{24} P(t).$$

Production estimates varied by ±5–22% when adjusted for errors in P–I parameter estimates (Table 1). Implicit in these computations is the assumption that no carbon loss from the particulates occurs during the incubation period. Although there is little justification for this assumption, an understanding of the magnitudes and sources of carbon losses in natural plankton assemblages is too limited at present to model these processes adequately (e.g. Peterson 1980; Eppley 1980). Model-derived production estimates should therefore approximate "gross" production since based on short-term ^{14}C incubations (Smith 1982; Smith and Platt 1984) and would be expected to equal or exceed SIS values under most conditions. Areal production estimates were computed, as in the case of SIS results, using a trapezoidal integration of P_v over the total depth interval sampled. Incubation temperatures in SIS deck boxes were generally 1–3°C higher than in the light-gradient boxes. For comparison of production rates, therefore, SIS values were corrected using an empirically derived production rate – temperature response curve (Li et al. 1984).

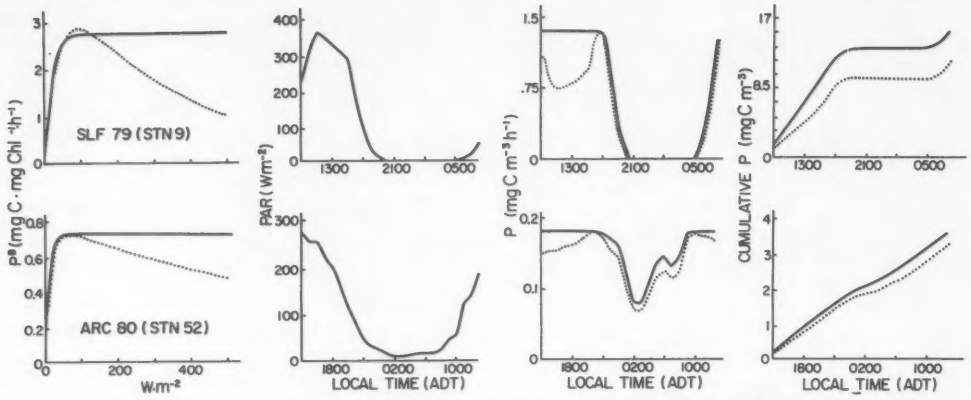

FIG. 1. Computational scheme used to derive primary production rates from P–I relationships (extreme left panel) and incident radiation (center, left panel). Examples are for surface (100% light level) samples using mixed-layer P–I parameters. Solid lines in far left and center and far right panels denote hyperbolic tangent model (HT, nonphotoinhibiting); dotted lines denote exponential (E, photoinhibiting) model. Center and far right panels show computed hourly and cumulative daily production rates, respectively.

Results and Discussion

Typical examples of model production estimates illustrating the computational scheme are given in Fig. 1. Two points are noteworthy in the results. First, the effects of model selection (i.e. photoinhibiting vs. nonphotoinhibiting) on hourly and cumulative production is evident, and second, regional differences in the time-course of carbon uptake are clear. The essentially constant production rate (i.e. linear carbon uptake) in arctic surface waters was at first unexpected because of the pronounced diel variation in incident radiation (Fig. 1, bottom). However, detailed time-course measurements using SIS methods confirmed this pattern (Li and Harrison 1982; Harrison 1983). In addition, more exhaustive comparisons of 4-h and 24-h measurements further suggested that nearly linear diel carbon incorporation was apparently a general feature of arctic waters (see also Herman 1983) in contrast with the conspicuously nonlinear pattern in temperate waters (Fig. 2).

Detailed comparisons by sample depth of model and SIS production estimates showed good agreement in most cases when model P–I parameters from the upper mixed layer were used; essential depth profile features were similar (Fig. 3). Production estimates from the exponential (photoinhibiting) model were generally about 10% lower than estimates from the hyperbolic tangent (nonphotoinhibiting) model. In the ARC 78 experiments, SIS production values fell between the two model estimates except at the surface; there, both model estimates were higher. Model values at the surface were also higher in the ARC 80 and SLF 79 experiments. In no case, however, were differences statistically significant (Table 2). Deviations were most obvious for the deepest (1% light level) samples in the ARC 80 and SLF 79 data (Fig. 3, 4). Here, SIS production rates were substantially higher than model estimates with differences being statistically significant (Table 2) even when errors in SIS and model production values were considered (see Methods). Areal production estimates (integrated over the euphotic zone), on the other hand, were not statistically distinguishable (Fig. 5; Table 2).

The systematically lower surface SIS values could be partially explained by time-dependent photoinhibition at high irradiances. Model production estimates incorporating a photoinhibition term (eq. 2) yielded values closer than nonphotoinhibiting model estimates although still higher than SIS values on the average. Light-gradient (model) populations were exposed to inhibiting light levels for 2–4 h whereas SIS populations were generally exposed to high irradiances for longer periods. The apparent increase in severity of photoinhibition with exposure time (e.g. Harris 1978, 1980; Goldman and Dennet 1984) may explain these differences. Others have observed a similar discrepancy between IS and model production estimates for near-

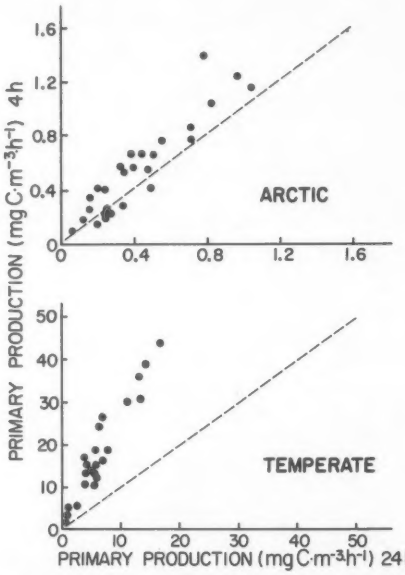

FIG. 2. Relationship between primary production rates computed using 4-h and 24-h incubations in SIS deck boxes, 50% light level. All incubations started near beginning of light period. Arctic data from Baffin Bay and surrounding waters, August 1980; temperate data from Bedford Basin, Nova Scotia, February–December 1978. Broken lines is 1:1 relationship and denotes linear carbon uptake rate; deviation from this line signifies progressive nonlinearity of uptake.

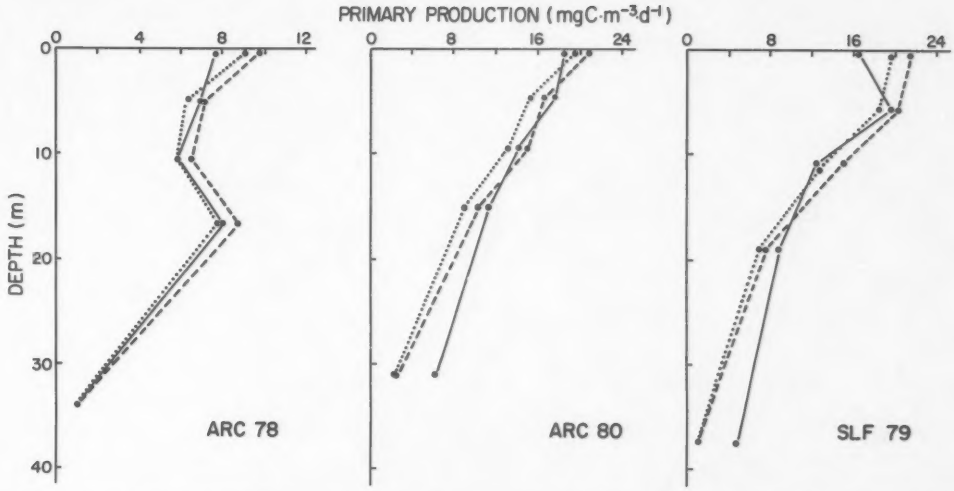

FIG. 3. Mean primary production rates in the euphotic zone comparing SIS with model estimates. Solid line = SIS, broken line = HT (nonphotoinhibiting) model, dotted line = E (photoinhibiting) model. P–I parameters from 50% light level.

TABLE 2. Linear regression analysis of hyperbolic tangent model (Y) and SIS (x) production estimates (**$P < 0.01\%$).

Cruise	Light depth (%)	No. of observations	Regression equation: $Y = mx + b$ $m(\pm SE)$	$b(\pm SE)$	Correlation coefficient (r)	df	t^a
ARC 78	100	12	1.65 (0.32)	−2.87 (2.87)	0.85	10	2.03
	50	12	1.15 (0.18)	−0.89 (1.53)	0.89	10	0.83
	25	12	1.59 (0.30)	−2.76 (1.87)	0.86	10	1.97
	10	12	0.97 (0.10)	0.91 (1.05)	0.95	10	−0.30
	1	12	0.97 (0.16)	−0.02 (0.19)	0.89	10	−0.19
	Σ	12	1.08 (0.20)	1.53 (39.89)	0.87	10	0.40
ARC 80	100	11	0.84 (0.16)	5.26 (4.15)	0.87	9	−1.00
	50	11	0.87 (0.12)	1.23 (2.73)	0.93	9	−1.08
	25	11	0.95 (0.12)	1.56 (2.05)	0.94	9	−0.42
	10	11	0.81 (0.15)	1.12 (2.00)	0.88	9	−1.27
	1	11	0.37 (0.03)	0.18 (0.34)	0.97	9	−21.00**
	Σ	11	0.80 (0.10)	34.77 (41.38)	0.93	9	−2.00
SLF 79	100	8	0.92 (0.26)	6.44 (5.27)	0.82	6	−0.31
	50	8	0.76 (0.18)	5.29 (4.35)	0.86	6	−1.33
	25	8	0.99 (0.27)	2.67 (3.92)	0.84	6	−0.04
	10	8	0.75 (0.32)	1.19 (3.27)	0.69	6	−0.78
	1	8	0.25 (0.06)	0.03 (0.35)	0.85	6	−12.50**
	Σ	8	0.78 (0.22)	67.68 (97.98)	0.82	6	−1.00

[a] t-value for testing difference of regression slope (m) from 1.0.

surface samples (e.g. Colijn et al. 1983). However, Gallegos et al. (1983) examined this question by experimentally exposing arctic marine phytoplankton to high (surface) light intensities, and then removing subsamples for analysis of P–I curve parameters. Rather than increasing in severity, the degree of inhibition diminished with time. Similar results were reported by Lewis et al. (1985b). The more general ecological significance of this often observed surface photoinhibition has been questioned (Harris 1978, 1980), with the implication that models excluding photoinhibition may provide the most realistic production estimates.

Likely, a more important explanation for the observed differences in surface SIS and model estimates may lie in the model assumption of conservation of assimilated carbon in the particulate matter (see Methods). Substantial losses of ^{14}C from particulates have been observed in diel (24-h) productivity experiments (e.g. Eppley and Sharp 1975) and almost certainly contributed to the lower observed SIS production values which were more representative of "net" production (e.g. Buckingham et al. 1975; Hobson et al. 1976; Marra et al. 1981; Smith 1982). Although tracer-recycling losses would occur at all depths, the discrepancy would probably be most evident in near-surface samples where carbon turnover rates are highest. Tracer losses during the relatively short-term (2–4 h) P–I incubations, on the

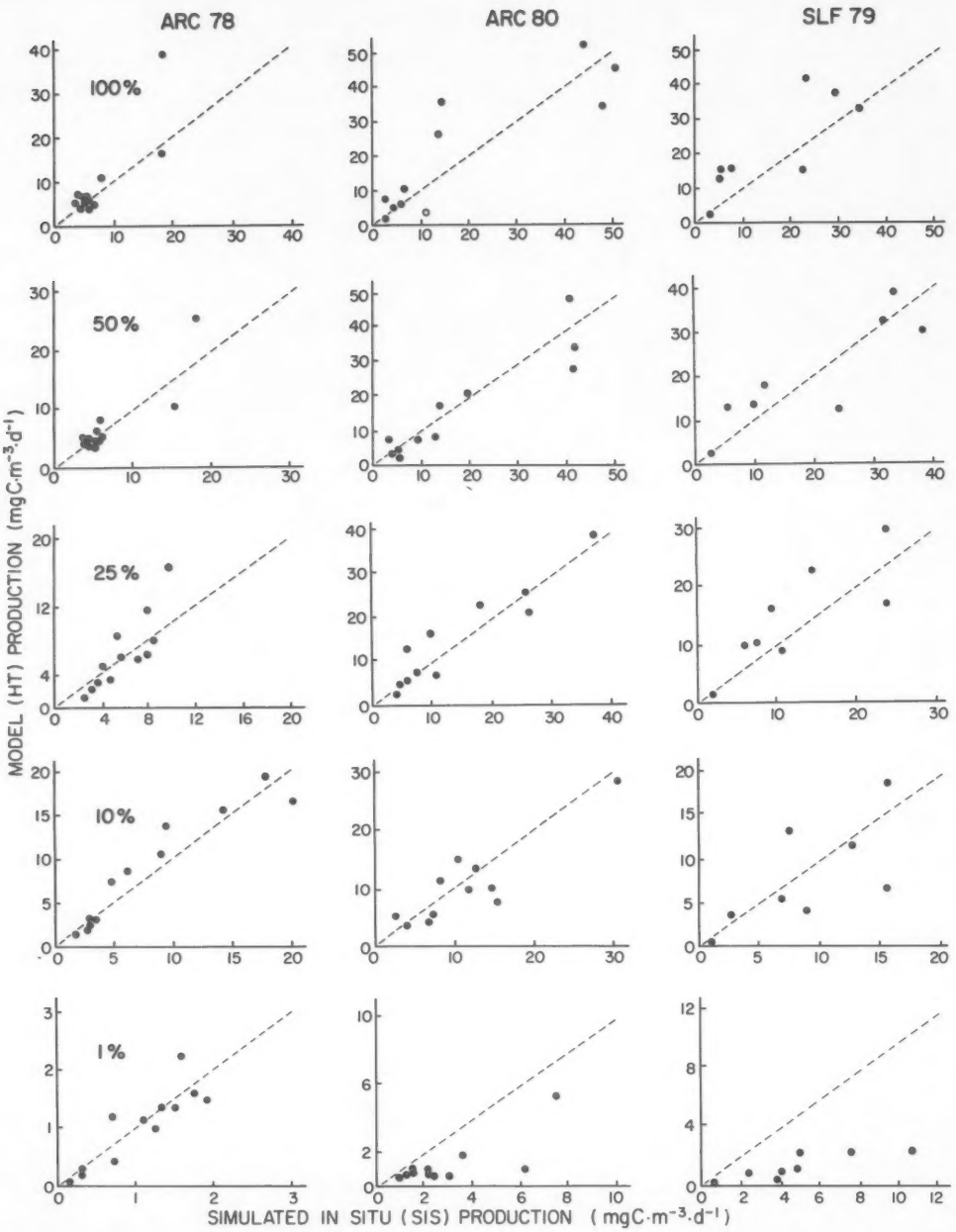

FIG. 4. Relationship between model (HT) and SIS production rate estimates for individual depths. Broken line is 1:1 relationship. P–I parameters from 50% light level.

other hand, were probably negligible (Smith 1982; Smith and Platt 1984). In environments where plankton growth rates are higher compared with the slow-growing high-latitude communities (Harrison et al. 1982; Li and Harrison 1982), tracer recycling and thus disparity between model and SIS production estimates would be expected to increase (see also Smith 1982).

Spectral or light quality differences also may have accounted for differences between SIS incubations having a solar light source and model estimates based on incubation under tungsten–halogen lamps. Plastic covers used in SIS incubations typically pass a large fraction of solar UV irradiation, some of which may pass the glass walls of incubation vessels. Tungsten–halogen lamps, on the other hand, emit light much less rich in the blue wavelengths; if one assumes that light must be absorbed to induce photoinhibition, then the increase in the pigment-absorbed blue light may account for an increase in photoinhibition in SIS incubations.

Several factors could have contributed to the disparity

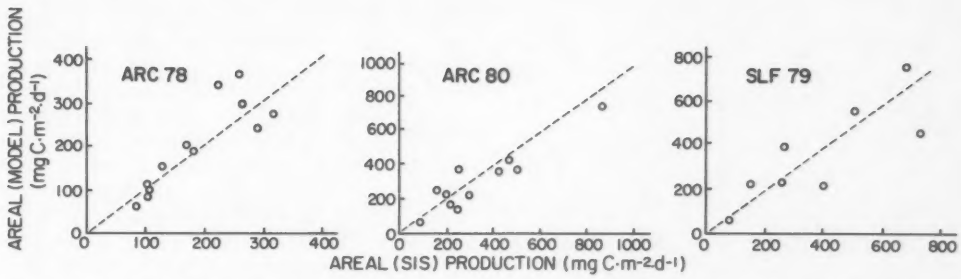

FIG. 5. Relationship between model (HT) and SIS areal production estimates. Broken line is 1:1 relationship. P–I parameters from 50% light level.

TABLE 3. Depth differences in P–I model parameters (units given in text). *Depth difference significant at the 95% confidence level; **significant at the 99% confidence level.

Cruise	No. of observations	Light depth (%)	P–I parameters: $\bar{x}$ (±SE)			
			P_s	P_m	α	β
ARC 78	12	50	1.50 (0.16)	1.42 (0.15)**	0.052 (0.003)**	0.0005 (0.0001)**
	12	1	1.34 (0.18)	0.84 (0.12)	0.039 (0.005)	0.0056 (0.0010)
ARC 80	8	50	1.20 (0.28)	1.07 (0.24)*	0.054 (0.010)*	0.0012 (0.0004)
	8	1	0.88 (0.11)	0.76 (0.10)	0.047 (0.008)	0.0016 (0.0004)
SLF 79	8	50	3.46 (0.49)	2.80 (0.31)**	0.056 (0.008)	0.0035 (0.0014)*
	8	1	3.25 (0.56)	1.91 (0.34)	0.044 (0.007)	0.0083 (0.0023)

TABLE 4. Comparison of model and SIS estimates of primary production (mg $C \cdot m^{-3} \cdot d^{-1}$) for individual light depths. Models using hyperbolic tangent (HT) equation and P–I parameters from the mixed-layer and 1% light level.

Cruise	No. of observations	Light level (%)	Model (mixed-layer), $\bar{x}$ (range)	Model (1% light level), $\bar{x}$ (range)	SIS $\bar{x}$ (range)
ARC 78	12	100	9.7 (4.2–38.8)	6.1 (1.8–30.0)	7.7 (3.8–18.2)
	12	50	7.1 (3.7–25.3)	4.5 (2.0–19.8)	6.9 (3.7–18.2)
	12	25	6.6 (1.4–16.6)	4.3 (0.9–13.3)	5.9 (2.6–9.8)
	12	10	8.7 (1.5–19.4)	5.7 (1.3–12.7)	8.0 (1.9–20.1)
	12	1	1.0 (0.1–2.2)	0.8 (0.1–1.5)	1.1 (0.2–1.9)
ARC 80	8	100	20.8 (2.3–52.2)	20.0 (3.5–40.2)	23.9 (4.6–50.5)
	8	50	16.7 (2.1–48.4)	15.8 (2.5–31.5)	22.3 (4.0–41.8)
	8	25	14.9 (2.5–38.7)	13.4 (4.1–23.1)	17.2 (4.6–37.0)
	8	10	10.3 (3.5–28.2)	8.9 (3.5–15.3)	13.7 (6.9–30.6)
	8	1	2.5 (0.6–13.9)	1.7 (0.6–7.2)	7.1 (1.3–37.3)
SLF 79	8	100	21.6 (2.6–41.4)	16.5 (1.8–33.1)	16.5 (3.4–34.4)
	8	50	20.3 (3.0–38.7)	16.0 (2.2–36.2)	19.7 (2.8–38.1)
	8	25	15.0 (1.7–34.6)	12.0 (1.5–25.7)	12.4 (1.9–25.7)
	8	10	7.9 (0.7–18.5)	6.0 (0.7–14.5)	8.9 (1.1–15.8)
	8	1	1.2 (0.1–2.4)	1.0 (0.1–2.9)	4.9 (0.6–10.6)

between model and SIS production estimates at low light levels. Some studies comparing IS and SIS incubations have attributed higher SIS values at low irradiances to a discrepancy between measured and true light levels inside the attenuated deck incubators (Jitts 1963; Brown 1982). Apparently, reflected light (both inside the incubators and from ship's superstructures) is not generally detected with the 2π geometry light sensors often employed in deck-box calibrations and may be particularly significant in the more attenuated incubators. Our SIS incubators have been calibrated with 2π and 4π light sensors, and light levels in the most attenuated boxes have typically deviated no more than ±20% from the nominally assigned values; this level of deviation would only partially explain the two- to four-fold difference we observed between model and SIS production rates at the 1% light level in the ARC 80 and SLF 79 experiments.

Spectral differences in light sources have also been suggested as a cause of divergent production estimates at low absolute irradiance levels (Jitts 1963; Kiefer and Strickland 1970).

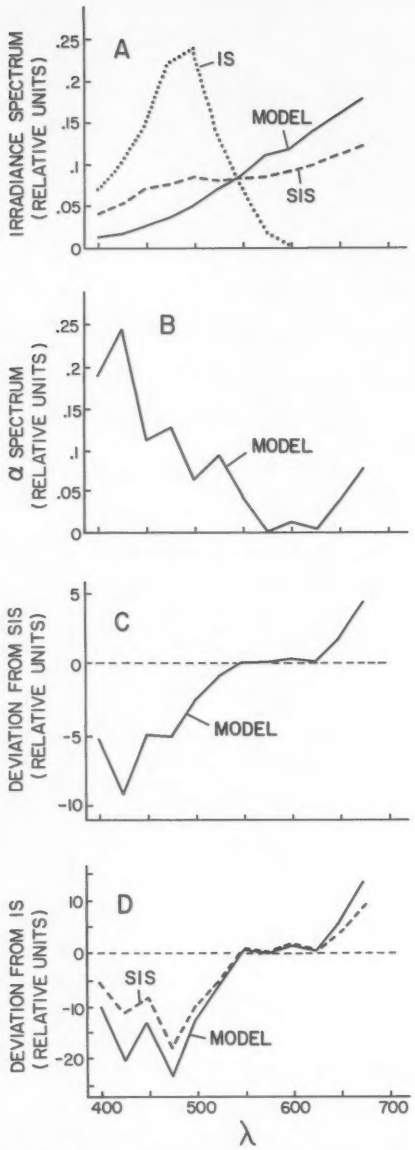

FIG. 6. Effects of spectral differences in light sources on estimates of primary production. (A) Irradiance spectra for P–I model and SIS incubators and IS light field at ~10% light level (~40 m depth). All values in relative units, i.e. integral = 1.0. (B) Typical photosynthetic action spectrum (α) for natural phytoplankton assemblage at ~40 m depth (see Lewis et al. 1985a, 1985b). (C) Deviation of P–I model production estimates (product of irradiance and α spectra) from SIS production estimates:

$$\int_{\lambda=400}^{700} \text{model: } \int \text{SIS} = 0.69{:}1.00.$$

(D) Deviations of P–I model and SIS production estimates from IS production estimates:

$$\int_{\lambda=400}^{700} \text{model: } \int \text{SIS}{:}\int \text{IS} = 0.43{:}0.62{:}1.00.$$

Recently developed methods for directly measuring photosynthetic action spectra of natural phytoplankton assemblages (Lewis et al. 1985a, 1985b) permit us to approximate the difference in model and SIS production estimates due to light quality alone. The P–I model incubator light source has a relatively lower proportion of blue and higher proportion of red light than does the neutrally attenuated solar spectrum of the SIS incubator (Fig. 6A). Furthermore, photosynthetic efficiency (α) typically has a major peak in the blue region and minor peak in the far red (Fig. 6B). As a consequence, the production rate (i.e. product of light and α spectra) from the P–I model incubator shows a pronounced negative deviation in the blue region and positive deviation in the red, resulting in an overall production value approximately 30% less than that from the SIS incubator (Fig. 6C). Using the same analysis, a comparison with the more conspicuously "blue" spectrum of the IS light-field at low irradiances (Fig. 6A) shows that model and SIS production estimates could be as low as 40 and 60%, respectively, of the IS production values (Fig. 6D). These results are consistent with the earlier work of Kiefer and Strickland (1970) and the more recent spectral analysis by Herman and Platt (1985). In our analysis, spectral errors were of minor significance for areal production estimates, since most of the production occurred near the surface (Fig. 3). However, disparity between model and IS production resulting from spectral differences would be expected to be greater in coastal or oceanic waters where a significant portion of the production occurs deep, i.e. in association with the subsurface chlorophyll maximum layer.

An additional explanation for these differences in production estimates at low irradiances may be that the P–I parameters, derived from mixed-layer populations, were inappropriate to characterize the light response of photosynthesis of the "deep" populations at the base of the euphotic zone (Fee 1973a, 1973b; Platt and Jassby 1976; Platt et al. 1982; Côté and Platt 1983). Model estimates using P–I parameters derived from 1% light-level populations, however, compared less favorably with SIS values than did the model estimates using the mixed-layer parameters. Consistently lower values of the P–I model parameters observed at the 1% light level (Table 3) resulted in model production estimates 10–50% lower than estimates using mixed-layer P–I parameters (Table 4); differences were most pronounced in the ARC 78 data. Adjustments in P–I parameters that would bring model estimates in line with the observed SIS values would require values of α (see eqs. 1 and 2) considerably larger than we have typically observed in arctic or temperate waters (W. G. Harrison and T. Platt, unpubl.). Herman and Platt (1985) have tested the utility of a similar chlorophyll–light model by comparing model-derived values with directly measured IS production rates. In this analysis, however, measured production rates were curve-fitted to the model production by adjusting the P–I parameters to obtain best-fit values of α and P_m. While there was some evidence that a depth-dependence of P–I parameters was required for a satisfactory model fit to experimental data at all depths, we concluded that the assumption of uniform P–I parameters throughout the photic zone was reasonable at most stations.

Despite the observed differences, absolute production estimates at the 1% light depth were small and consequently contributed little to the overall column production. Areal production rates from model and SIS incubations showed good agreement (Fig. 5; Table 2). Of the models and choice of P–I parameters tested, the nonphotoinhibiting (HT) model using mixed-layer P–I parameters compared best considering all data

TABLE 5. Comparison of model (HT, E) and SIS areal primary production estimates (mg $C \cdot m^{-2} \cdot d^{-1}$).

Cruise	No. of observations	Light level (%)		Primary production rate, $\bar{x}$ (range)
ARC 78	12		SIS	185 (84–313)
	12	50	HT	203 (63–363)
	12		E	182 (57–325)
	12	1	HT	134 (57–271)
	12		E	122 (53–248)
ARC 80	11		SIS	337 (91–860)
	11	50	HT	304 (62–745)
	11		E	275 (56–680)
	11	1	HT	272 (117–413)
	11		E	246 (107–379)
SLF 79	8		SIS	383 (80–728)
	8	50	HT	365 (61–764)
	8		E	331 (53–699)
	8	1	HT	288 (50–597)
	8		E	267 (46–551)

TABLE 6. Analysis of variance in model generated areal production estimates. *Significant at 95% confidence level. P–I parameters tested were those derived from the mixed-layer (50% light level) and from the 1% light level. P–I models tested were the nonphotoinhibiting (HT) and photoinhibiting (E) equations.

Cruise	Source of variability	df	*F*
ARC 78	P–I parameters	1	7.0*
	P–I models	1	0.4
	Residuals	45	
ARC 80	P–I parameters	1	2.1
	P–I models	1	0.3
	Residuals	29	
SLF 79	P–I parameters	1	0.9
	P–I models	1	0.1
	Residuals	29	

(Table 5), although the slightly lower estimates using the photoinhibiting equation (E) were not statistically significant (Table 6). P–I parameters from the 1% light level generally provided poor model estimates of column production, significantly (95% confidence level) underestimating SIS values in the ARC 78 data (Table 6).

Our results strengthen conclusions from earlier studies (Fee 1973a, 1973b; Jitts et al. 1976) that model methods for computing primary productivity offer a valuable alternative to conventional methods (i.e. IS or SIS incubations) while also providing (through P–I parameters) more physiological information than available from water column profiles (Platt and Jassby 1976). Recent advancements in continuous measurement of light and chlorophyll now provide the capability to construct highly resolved (vertical and horizontal) productivity data, using model methods, not previously possible with conventional incubation techniques (Herman and Platt 1983; Herman 1983, 1984; Herman and Platt 1985). Furthermore, we suggest that P–I parameters chosen from a single depth stratum (upper mixed-layer) may be adequate in most cases to estimate total column production even under conditions of vertical stratification.

One of the most significant shortcomings of our model method seems to be our lack of proper matching of incubator light quality with that observed in situ. This results in a systematic and often significant underestimation of production at low absolute irradiance levels (although this may have little effect on column production estimates). However, model parameters derived from spectrally adjusted P–I incubators (Lewis et al. 1985a, 1985b) will help alleviate these errors.

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Use of Pup Counts in Indexing Population Changes in Pinnipeds

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Berkson, J. M., and D. P. DeMaster. 1985. Use of pup counts in indexing population changes in pinnipeds. Can. J. Fish. Aquat. Sci. 42: 873–879.

A series of population simulations were used to test the accuracy of estimating the discrete rates of population change (RPC) from annual pup counts. The simulations indicate that pup counts can give a biased estimate of RPC, and that the magnitude and direction of bias depends on which life history parameters are density dependent and on the maximum rate of population change. In general, if pre-census pup survival is density dependent the estimated RPC using pup counts is too low. If post-census pup survival is density dependent, the estimated RPC is too high. If adult survival is density dependent, there is very little bias in the estimate. The results indicate that pup counts can be reliable indicators of population growth, but caution should be used in interpreting the results unless density feedback mechanisms have been identified.

Les auteurs utilisent une série de simulations démographiques pour vérifier la précision des estimations des taux discrets de variation d'une population (TVP) effectuées à partir des recensements annuels de nouveaux-nés. Les simulations révèlent que ces dénombrements peuvent fournir une estimation biaisée du TVP et que les paramètres vitaux dépendant de la densité et le taux maximum de variation d'une population influent sur l'ampleur et la direction de la tendance. En général, le TVP calculé en fonction des recensements de nouveaux-nés est trop faible si la survie de ceux-ci avant le dénombrement dépend de la densité. Par contre, le TVP est trop élevé si la survie après le dénombrement dépend de la densité. L'estimation est très peu biaisée si la survie des adultes dépend de la densité. Les résultats révèlent que le recensement des nouveaux-nés constitue un indice fiable de la croissance démographique ; on doit toutefois interpréter les résultats avec prudence à moins d'avoir trouvé des mécanismes rétroactifs liés à la densité.

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For many species of pinnipeds, annual counts of pups provide the best available censusing method. These counts are used to estimate the rate of population change (RPC) by comparing percentage change in counts from year to year as in the case of California sea lions, *Zalophus californianus* (DeMaster et al. 1982); northern elephant seals, *Mirounga angustirostris* (Antonelis et al. 1981; Cooper and Stewart 1983); and Antarctic fur seal, *Callorhinus ursinus* (Chapman 1961; Eberhardt 1981; Fowler 1982). Recently, methods that rely on pup counts have also been developed to estimate whether the population is above or below the maximum net productivity level (MNPL), the point where the net growth rate of the population is maximized (DeMaster et al. 1982).

In this paper, an age structured simulation model is used to evaluate the accuracy of predicting population trends from a time series of pup censuses. We have assumed that the sex ratio of pups at birth does not change with population size, and therefore, models that utilize female pups only are suitable for predicting the direction and magnitude of bias in using pup counts to estimate the RPC. Possibly, biases in estimating RPC's with pup counts exist, and these biases may differ under different life history scenarios. If we can understand these biases and their causes, we can increase the predictive powers of the pup counts, or at least be aware of the limits when using pup counts to manage resources.

In the simulations we use life history parameters that are representative of most populations of pinnipeds (Eberhardt and Siniff 1977). The number of individuals in the first age class (1) is defined as the number of female pups at the time the census is made. In developing the model, three mechanisms of density dependence were investigated: density-dependent post-census pup survivorship, dependent on the number of pups in the population; density-dependent pre-census survivorship, dependent on the number of births in the population; and density-dependent adult survivorship, dependent on the number of non-pups in the population. Both types of pup survival are considered to be the most likely types of density dependence in the wild (Eberhardt 1977). Adult survival was selected because the population growth rate is most sensitive to its change (Goodman 1978, 1984). Fecundity and age at maturation were not investigated in depth because, as will be shown, they would provide the same sort of bias as does density dependence in pre-census pup survival. For simplicity, all types of density dependence were treated as linear functions.

Methods

Our age structure population models were written in the FORTRAN programming language. Initial parameters were selected to produce either an 8% or a 4% growth rate. These RPC's were considered reasonable for recovering populations of pinnipeds (Eberhardt and Siniff 1977). The model was

TABLE 1. Selected pinniped life history parameter values of given age classes (*denotes minimum values).

	Weddell seal[a]	Antarctic fur seal[b]	NW Atlantic harp seal[c]	Gray seal[d]
Annual survival rates of given age classes				
Birth–weaning		0.85		0.73
Weaning – age 1				0.90
Birth – age 1	0.76–0.82*	0.76–0.92	0.50–0.97	
Juvenile	0.48–0.50*	0.95		0.93
Adult	0.66–0.76*	0.92–0.95	0.90	0.94
Annual fecundity rates of given age classes				
Age 3	0.27	0.28		
Age 4	0.27	0.38		0.08
Age 5	0.27	0.42		0.28
Age 6 and older	0.40	0.45	0.46	0.42

[a]Stirling (1971).
[b]Payne (1977, 1979).
[c]Lett et al. (1981).
[d]Harwood (1981).

designed to handle a population with 25 year–age classes (Eberhardt and Siniff 1977). The probability of surviving through age class 25 was set at 0. A sample of life history parameter values reported for pinnipeds is listed in Table 1. The range of life history values used in the simulations is listed in Table 2.

The age classes followed a trajectory based on the following equations:

$$N_{1,t+1} = \sum_{x=1}^{25} N_{x,t} \cdot M_x$$

$$N_{x+1,t+1} = N_{x,t} \cdot P_x \qquad x = 1, 2, \ldots, 24$$

where P_x = the probability of survival from census at age x until census at age $x + 1$ and M_x = the probability of a female age x at year t having a female offspring at year $t + 1$.

For each case, the population level was initially set at 25% of the carrying capacity and allowed to continue to equilibrium. The RPC at time t was estimated by calculating

$$\text{RPC (total population)} = N_t/N_{t-1}$$

$$\text{RPC (pups)} = N\text{pups}_t/N\text{pups}_{t-1}.$$

The net population change was calculated as

$$\text{Delta (total population)} = N_t - N_{t-1}$$

$$\text{Delta (pups)} = N\text{pups}_t - N\text{pups}_{t-1}.$$

The bias of estimating the RPC by the pup growth rate was calculated as

$$\text{Bias} = \frac{\text{RPC (pups)} - \text{RPC (total population)}}{\text{RPC (total population)}}.$$

The three types of density dependence were tested with initial RPC's of 8 and 4% to see if changing the rate at which equilibrium is achieved changes the bias. Density-dependent post-census survival was calculated in the following way:

$$P(1, t) = P(1, k) + [P(1, i) - P(1, k)] \times \left[1 - \frac{N(1, t) - N(1, i)}{N(1, k) - N(1, i)}\right]$$

TABLE 2. Parameter values used in density dependence simulations.

	Model 1 (post-census pup survival)	Model 2 (pre-census pup survival)	Model 3 (adult survival)
Annual survival rates of given age classes			
Birth–census	1.00	0.40–1.00	1.00
Census – age 2	0.30–0.75	0.75	0.75
Age 2	0.85	0.85	0.85
Age 3	0.90	0.90	0.90
Age 4 – age 24	0.94	0.94	0.84–0.94
Annual fecundity rates of given age classes			
Age 4	0.10	0.04–0.10	0.09–0.10
Age 5	0.20	0.08–0.20	0.18–0.20
Age 6	0.30	0.12–0.30	0.27–0.30
Age 7 – age 24	0.40	0.16–0.40	0.36–0.40

where $P(1, t)$ = survival of age class 1 at time t, $N(1, t)$ = population of age class 1 at time t, k = time at which population is at carrying capacity, and i = time at which population is initially started.

Density-dependent pre-census survival was calculated in the following way:

$$G(t) = G(k) + [G(i) - G(k)] \cdot \left[1 - \frac{N(B, t) - N(B, i)}{N(B, k) - N(B, i)}\right]$$

where $G(t)$ = pre-census survival rate at time t and $N(B, t)$ = number of births at time t calulated by

$$N(B, t) = \sum_{x=1}^{25} F(x) \cdot N(x, t) \cdot P(x)$$

where $F(x)$ = fecundity for age class x conditional on female survival, $N(x, t)$ = population in age class x at time t, and $P(x)$ = survival of age class x.

Once $G(t)$ was calculated, it was used in the following equation to calculate the effective fecundity (Goodman 1984) for

TABLE 3. Results of density dependence simulations with three models. (RPC = rate of population change, MNPL = maximum net productivity level, EPL = equilibrium population level).

	Model 1 (post-census pup survival) initial growth rate		Model 2 (pre-census pup survival) initial growth rate		Model 3 (adult survival) initial growth rate	
	8%	4%	8%	4%	8%	4%
Percentage of EPL at true MNPL	68	58	67	58	52	52
Percentage of EPL at predicted MNPL	78	63	48	47	49	50
Percentage of EPL at predicted MNPL minus percentage of EPL at true MNPL	10	5	−19	−11	−3	−2
Bias in RPC at true MNPL	0.009	0.002	−0.018	−0.005	−0.002	−0.001
Largest bias in RPC	0.011	0.002	−0.027	−0.006	−0.002	−0.001
Time lag in years between true MNPL and predicted MNPL	−3	−3	+6	+7	+1	+1
Largest time lag in years	−4	−4	+15	+12	+3	+1

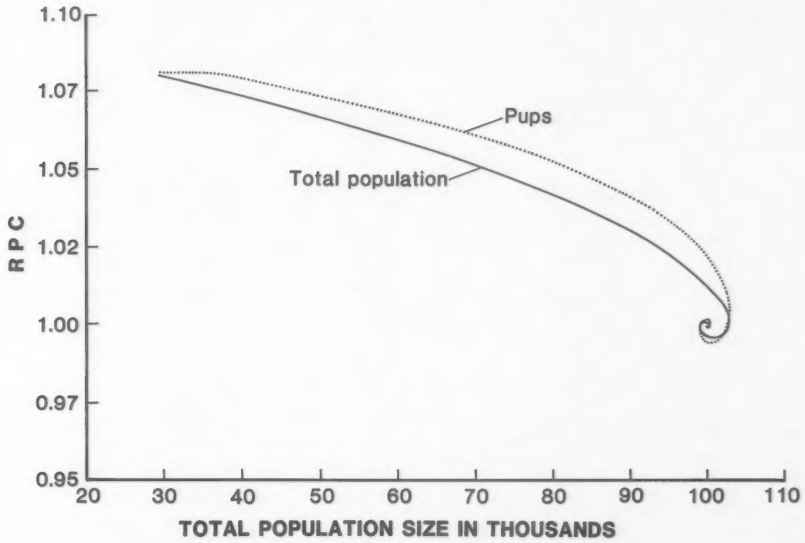

FIG. 1. Relationship of the RPC and the total population size when post-census pup survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

use in the Leslie matrix:

$$M(x, t) = F(x) \cdot P(x) \cdot G(t)$$

where $M(x, t)$ = effective fecundity of age class x at time t.

Density-dependent adult survival was calculated in the following way:

$$P(A, t) = P(A, k) + [P(A, i) - P(A, k)] \times \left[1 - \frac{N(NP, t) - N(NP, i)}{N(NP, k) - N(NP, i)}\right]$$

where $P(A, t)$ = survival of adult age classes at time t (adult age classes are 4 through 25) and $N(NP, t)$ = number of non-pups in the population at time t calculated by

$$N(NP, t) = \sum_{x=2}^{25} N(x, t).$$

The adult survival rate at time t was used to calculate $M(x, t)$ at each iteration of the simulation.

Results

Results of the six different simulations indicate that biases in estimating the RPC depends on the type of density dependence and the magnitude of the maximum RPC. Additionally, biases found in estimating the time when the MNPL is reached also depend on the type of density dependence and the magnitude of the RPC. Simulation results are discussed in three sections: density-dependent post-census pup survival (model 1), density-dependent pre-census pup survival (model 2), and density-dependent adult survival (model 3). A summary of results is provided in Table 3.

Density-Dependent Post-Census Pup Survival

When post-census pup survival is density dependent, the total population reacts more quickly than the pup population to the effects of the density dependence. Density-dependent post-census pup survival affects the number of individuals in the first

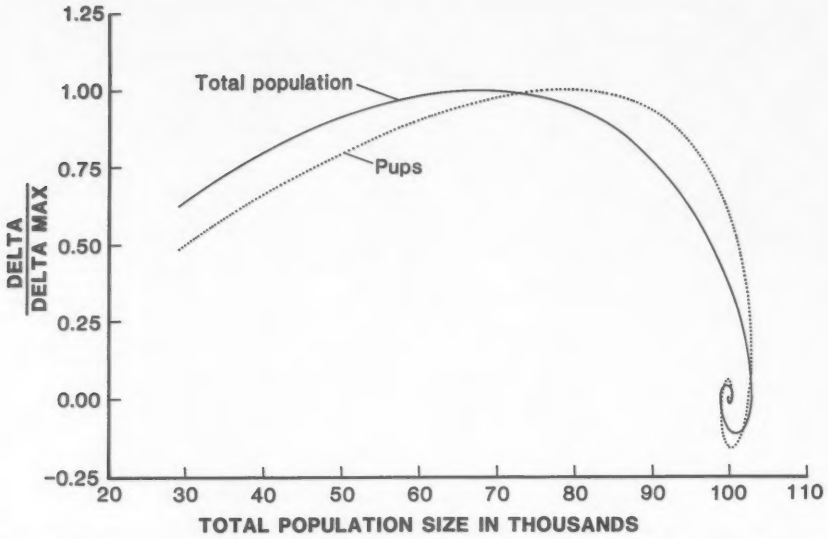

FIG. 2. Relationship of predicted and true production curves to total population size when post-census pup survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

age class that survive to the second age class. Therefore, any drop in survivability immediately acts on the number of individuals entering the second age class and, in doing so, acts on the total population as well. The first age class does not respond to the effects of the density dependence until the cohort that originally entered the second age class becomes capable of reproducing. Thus, the dynamics of the pup population lag behind the total population as the RPC declines (Fig. 1).

For the same reason, the production curve determined by pup counts lags behind the production curve of the total population (compared by measuring delta/delta max in both curves) (Fig. 2). In this case, delta max is the maximum change in the production curve.

In both the 8 and 4% growth simulations, the RPC of the pups lags behind the RPC of the total population. The time lag between the pups and the total population is the same in both simulations. However, the high initial RPC simulated population grows much larger during the time lag than the low initial RPC population. The difference between the true MNPL and the MNPL as indicated by the pup counts is larger for those simulations using higher initial rates of increase.

Density-Dependent Pre-Census Survival

In the case of density-dependent pre-census survival, the bias is in the opposite direction from that in the case of density-dependent post-census pup survival. Once again this bias can be explained to be a result of density dependence acting on a specific part of the age structure. Any decrease in pre-census survival immediately acts on the population in the first age class. The effect of this decreased survival is an immediate decline in the RPC of the number of pups. The RPC of the total population also declines but to a lesser degree, due to the buffering of the 24 unaffected age classes (Fig. 3). Once again the production curves also show this time lag (Fig. 4).

The 4% initial growth simulation again shows the same direction of bias as found in the 8% simulation. The magnitude of the bias in terms of time lags in the two production curves is similar, although in the 4% simulation it is slightly less than in the 8% simulation. This translates into a smaller population difference between the two peaks of the production curves, due again to the lower population increase in the same amount of time as seen in the simulation with 4% initial growth.

Density-Dependent Adult Survival

In the case of density-dependent adult survival, the decreasing survival rate affects both the adult age classes (5–25) and the pup age class (1). Therefore, a much smaller bias is created. This is because adult survival affects the number of pups entering the first age class the following year. Any given decrease in adult survival affects all age classes other than the juveniles (ages 2, 3, and 4) in the next time step. Having three age classes with unchanging survival rates in turn causes the total population's RPC to decline slightly behind the pup population's RPC (Fig. 5). The magnitude of this bias is much smaller than is seen in the previous two types of density dependence. Once again, the production curves follow this same pattern (Fig. 6).

Discussion

The simulations we described indicate that the type of density dependence affecting a population can bias estimates of RPC based on pup counts. For example, estimates of replacement yield and MNPL that rely on pup counts are probably biased. The direction of bias, however, can be inferred if the density-dependent mechanisms are known.

Managers should be aware of these biases and should incorporate them in the development of management policy. The following comparisons of density dependence found in the wild and its effects on estimating population changes using simultations will, hopefully, illustrate this point.

To infer a direction of bias in the use of pup counts to estimate

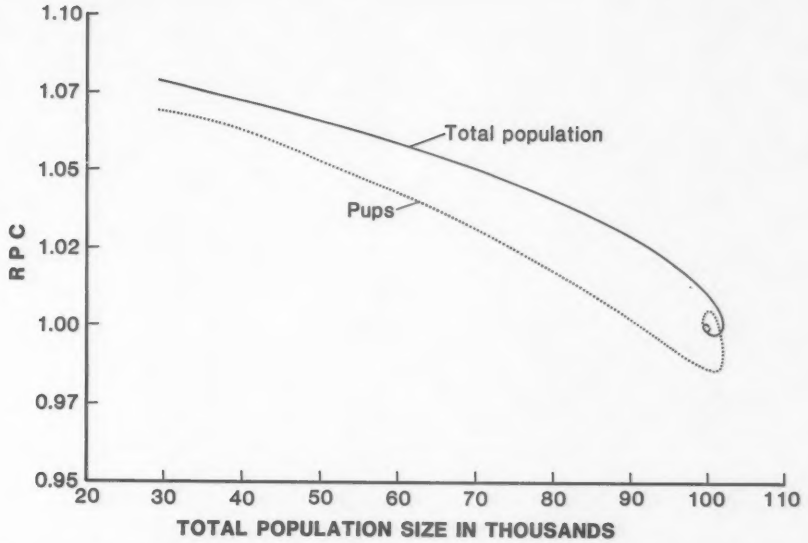

FIG. 3. Relationship of the RPC and the total population size when pre-census pup survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

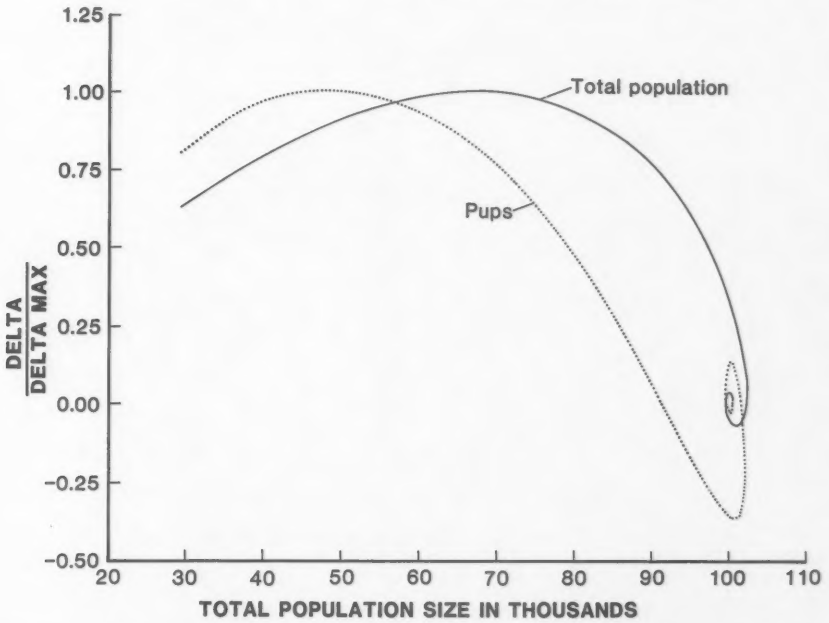

FIG. 4. Relationship of predicted and true production curves to total population size when pre-census pup survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

the RPC, it is reasonable to look at the available data on what parameters are density dependent in pinnipeds. Eberhardt (1977) suggested that pup survival (both pre- and post-census) is more likely to be density dependent than either adult fecundity or adult survival. Adult fecundity would cause the same direction of bias as pre-census pup survival, since both act on the first age class. However, because pre-census pup survival is more likely to be density dependent than adult fecundity (Eberhardt 1977), it was chosen for modeling.

Density-dependent pup production has been described in many pinniped species (for summary see Fowler et al. 1980). For gray seal, *Halichoerus grypus*, this mechanism has been described to act on pups between the age of birth and weaning (Coulson and Hickling 1964; Bonner 1975; Harwood 1981).

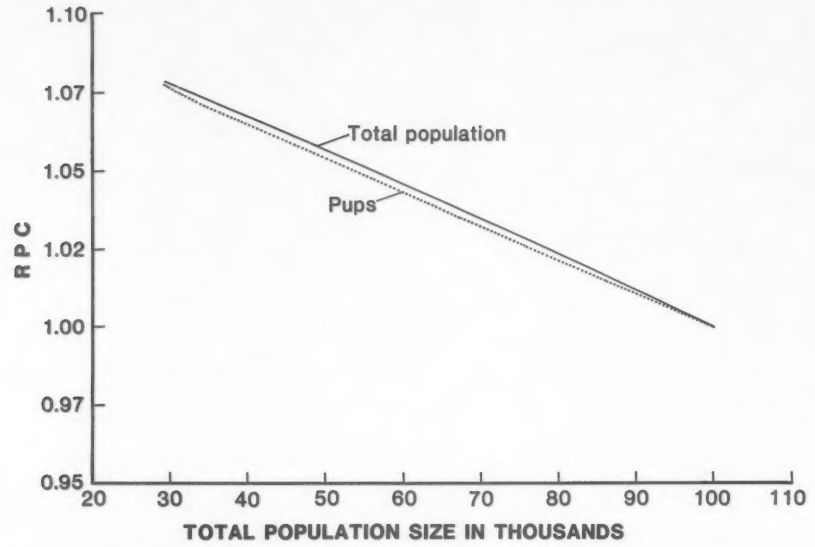

FIG. 5. Relationship of the RPC and the total population size when adult survival is density dependent. Dotted line represents RPC of total population as predicted by pup counts.

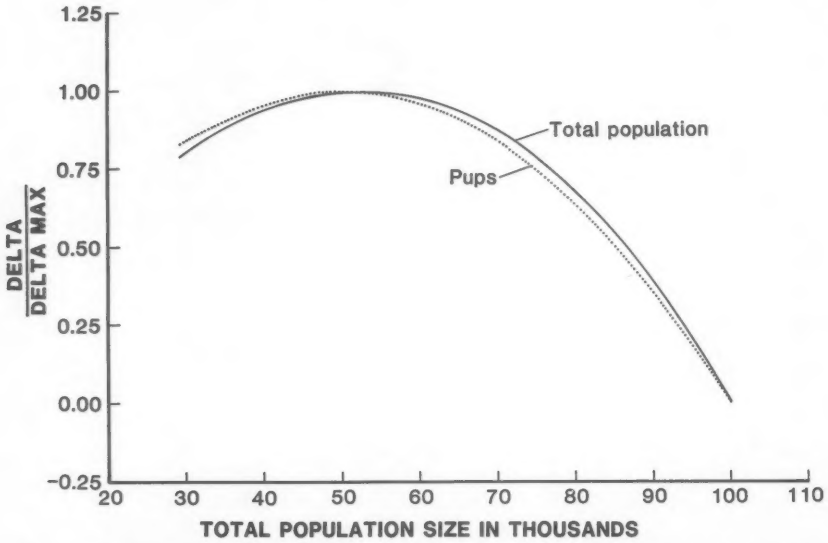

FIG. 6. Relationship of predicted and true production curves to total population size when adult survival is density dependent. Dotted line represents production curve of total population as predicted by pup counts. Data are based on initial RPC of 8%.

Density-dependent birth rates have been described in northwestern Atlantic harp seals, *Phoca groenlandica* (Lett and Benjaminsen 1977; Lett et al. 1981). Northern fur seals were the first of many pinniped species to have shown evidence of density-dependent age at maturation (Scheffer 1955). In all three types of density dependence described, the density dependence is assumed to act on the first age class and would cause the pup population to lead the total population both in the decline of the RPC and in passing the peak on the production curve as shown in the pre-census pup survival model.

The results of the two simulations where pre-census survival is density dependent indicate that pup counts provide a conservative estimate of the RPC. This absolute value of bias can be as high as 3% in the case of an initial growth rate of 8%. In addition, using pup counts to determine whether a population is above or below the MNPL is not conservative. That is, pup counts (under this type of density dependence) indicate that a population is above the MNPL before the population actually reaches the MNPL.

Density-dependent juvenile survival has been reported in pinnipeds, as in the northwestern Atlantic harp seal (Lett and Benjaminsen 1977; Lett et al. 1981). In this case, density

dependence acts on the juvenile age classes rather than on the first age class. This would cause the pup counts to trail the total population both in the decline in the RPC and in passing the peak on the production curve as demonstrated above in the post-census simulation.

In both simulations where post-census pup survivorship is density dependent, pup counts lag behind the total population, or in other words, pup counts overestimate the true RPC of the population and are late in estimating the time at which peak productivity occurs. The largest bias in the RPC is one percentage point; it occurs in the vicinity of the MNPL. The bias in estimating peak production is −3 yr. This means that if post-census survival is density dependent, pup counts are conservative in indicating whether or not a population is above or below its MNPL.

Evidence of density-dependent adult survival in pinnipeds is difficult to obtain, if it does exist, due to the complications in obtaining accurate data. For those species where it is demonstrated to occur, pup counts would be accurate in predicting the population RPC and the relative position on the production curve as was seen in the adult survival model.

Possibly more than one type of density dependence may be operative (Smith and Polacheck 1981). Given the mechanisms we have proposed in this paper (i.e. pre-census pup survival and post-census pup survival) the resultant bias would be a combination of the two independent biases and would self-cancel to some extent.

Possibly, nonlinear density dependence is a more reasonable mechanism than linear density dependence (Fowler 1981). The difference in bias between models with linear and nonlinear density dependence would clearly be in magnitude rather than direction. The difference in resulting bias is unknown at this time. Future work will address these issues.

In order to use the predictions of this paper, managers need to know the type of density-dependent mechanisms acting on the population. If the density dependence acts on the pups, either through adult fecundity, age at maturation, or pup survival prior to census, the bias would cause the pup population to lead the total population both in the decline of the RPC and in passing the peak on the production curve. If the density dependence acts on the pups after census, the pup population would trail the total population both in the decline of the RPC and in passing the peak on the production curve.

We conclude with a particular example of how the results of our study can be used to determine the status of a stock from pup counts. It has been suggested that the San Miguel Island population of California sea lions is above the MNPL (DeMaster et al. 1982). Based on data from the years 1975 to 1981 on San Miguel Island (DeMaster et al. 1982), a regression of the survival rate of pre-census pups versus number of pups born did not show a slope significantly different from zero. In addition, most of the sea lions that are "salvaged" by rehabilitation centers each spring are yearlings in an emaciated condition. This was particularly evident in the spring of 1983, when winter storms were unusually severe. If we can assume that post-census survival is density dependent and that pre-census survival is not affected by density, then we can increase our confidence in this status assessment based on the conclusions of our model. In this case, the population should be even closer to the equilibrium population level than is indicated by the pup counts.

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Atlantic Herring (*Clupea harengus*) Distributions in the Gulf of Maine – Scotian Shelf Area in Relation to Oceanographic Features

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Sinclair, M., and T. D. Iles. 1985. Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine – Scotian Shelf area in relation to oceanographic features. Can. J. Fish. Aquat. Sci. 42: 880–887.

There are clear, temporally persistent patterns in the spatial distributions of Atlantic herring (*Clupea harengus*) at various life history stages. Three areas of potential importance for summer feeding and overwintering and one juvenile nursery area are described. In contrast, there are several well-defined spawning locations and larval distributional areas. The distributional patterns infer considerable between-population mixing at all phases of the life history except at spawning time itself and during the first several months of the larval phase. The life history distributions are interpreted in relation to tidally induced oceanographic features of the area. The specific locations of spawning and the associated larval distributions are interpreted to be a function of the location of physical features associated with "larval retention." The summer-feeding areas are associated with the location of tidally induced temperature fronts where plankton production is high. The larval distributional areas are argued to be occupied in spite of their particular plankton characteristics rather than because of them. The observed distributions are not consistent with some fisheries biology theories.

Les répartitions spatiales des divers stades vitaux du hareng de l'Atlantique (*Clupea harengus*) présentent des régimes distincts et temporellement répétés. Le présent rapport décrit trois zones potentiellement importantes pour l'alimentation en été et l'hivernage, et une zone d'alevinage. Il existe par contre plusieurs frayères et aires de répartition des larves bien définies. Les schèmes de répartition indiquent un important mélange entre les populations à tous les stades du cycle vital, sauf pendant la fraie et au cours des premiers mois de la phase larvaire. On interprète la répartition des stades vitaux en fonction des caractéristiques océanographiques liées à la marée dans cette région. Ainsi, l'emplacement précis de la fraie et la répartition subséquente des larves sont perçues comme fonction de l'emplacement des particularités physiques associées à la rétention des larves. Les zones d'alimentation estivale correspondent à des fronts thermiques provoqués par la marée où la production planctonique est élevée. On soutient que les zones de répartition des larves sont occupées malgré leurs caractéristiques particulières pour ce qui est du plancton et non à cause de celles-ci. Les répartitions observées ne sont pas en accord avec certaines théories de l'halieutique.

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The first comprehensive study of Atlantic herring (*Clupea harengus*) in Canadian waters was undertaken by the Norwegian pioneer of fisheries oceanography, Johan Hjort, and his co-workers during the Canadian Fisheries Expedition in 1914–15. The aims of the expedition in general, and the herring studies in particular, were to address "the problems which had ranked foremost in the Scandinavian marine researches of the (previous) generation, to wit, the relation between the distribution and life cycle of the organisms, on the one hand, and the prevalent physical conditions on the other" (Hjort 1919). The questions asked in this paper are the same as those addressed by Hjort over 60 yr ago. In fisheries ecology such formally simple questions whose answers involve descriptions of distributions and their empirical analysis have lost favor in recent decades as the systems approach and modelling techniques have become the vogue. This change in orientation is perhaps due to the general failure of descriptive studies to generate explanatory power, and the substitution of the aim of understanding by the hope of prediction (Pielou 1981). The state of the art of physical oceanography, however, and appreciation of its precise role in the control of the phytoplankton component of the pelagic ecosystem at least, has progressed considerably during the past decade (Pingree et al. 1975, 1976, 1977). In the light of this progress in the oceano-

graphic field it seems possible that re-asking old questions may lead to new insights.

In this paper the distributions of Atlantic herring within the Gulf of Maine – Scotian Shelf area are initially described. From the extensive herring tagging experiments in this study area over the past decade it has been observed that there is limited movement of herring from the Gulf of Maine area either across the Laurentian Channel or into the Gulf of St. Lawrence (Stobo 1983). Thus it is reasonable to treat this geographic area (Fig. 1) as a natural unit for herring. Certain physical and biological oceanographic features of the various herring distributional areas are subsequently reviewed. Finally, the combined herring and hydrographic empirical observations are discussed in relation to a recent stock hypothesis for herring (Iles and Sinclair 1982).

Data Sources

Data on fisheries distributions come from a wide range of sources including landing statistics, fishermen's logs, and port samples. Unlike many field or laboratory experiments it is difficult to verify the accuracy and directions of bias of much of the sampling methodology. Nevertheless, there is an accumulated body of "soft" data on distributions of commercially exploited fish populations that exceeds by far that generally available for noncommercial species. Much of this class of data is used here in this synthesis on herring distributions in the Gulf of Maine – Scotian Shelf area. In our view (given reasonable judgement in the treatment of the data) the information content in the accumulated fisheries data outweighs the noise caused by the uncertainties in the collection procedures.

The distribution of adult summer-feeding herring was summarized from three main sources: an unpublished Russian fishing atlas entitled *Industrial Description of Trawling, Drift Net and Purse-Seining in the Region of the Atlantic Along the Coast of the United States and Canada* (in Russian) (a copy of the atlas can be borrowed from the senior author); the logbooks of the Canadian purse-seine fleet (on file at the Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, N.S.) during their summer fishing (principally June to July) off southwest Nova Scotia during the years 1968–81; and the fishing reports summarized by Huntsman (1953) for the Grand Manan area. The information on the timing of formation of prespawning aggregations and their geographic location was derived from analysis of the southwest Nova Scotia drift–gill net fishery landing statistics. The fishery starts each year in relation to the prespawning behavior. Daily landings for this gear type were analysed for southwest Nova Scotia for the years 1977 and 1978.

Locations of spawning were derived from diverse sources. The Georges Bank and Nantucket Shoals spawning locations are inferred from actual spawning fishery locations identified in the Russian fishing atlas mentioned above, from Anthony and Waring (1980) and unpublished gonad development state analyses carried out by H. Dornheim (Institut für Seefischerei, Federal Republic of Germany, pers comm.) on samples taken from the Federal Republic of Germany fishery, and from published reports of direct observations from a submersible (Caddy and Iles 1973). The three Gulf of Maine nearshore spawning locations were identified by J. Graham (Boothbay Harbor, ME, pers. comm.) from his extensive observations on the distribution of recently hatched yolk sac larvae along the coast of Maine. Since there are no commercial fisheries on these

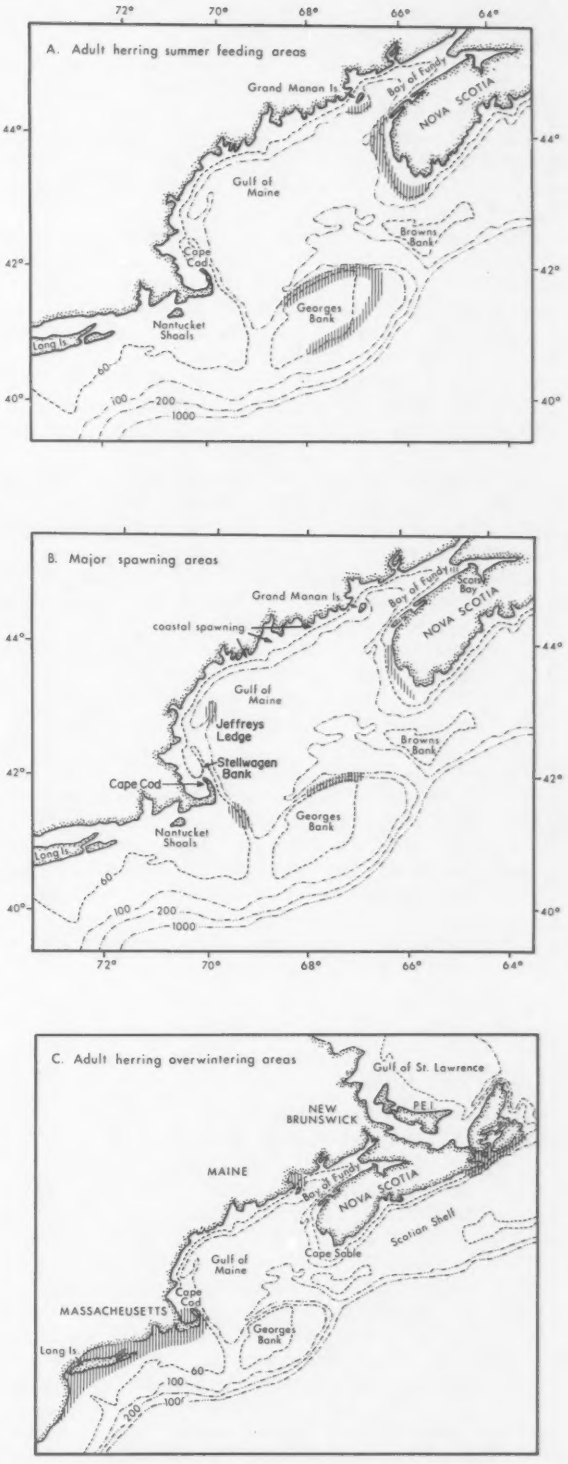

FIG. 1. Adult herring distributions within the Gulf of Maine – Scotian Shelf area. (A) Summer-feeding distribution; (B) spawning location distribution; (C) Overwintering distribution.

inferred spawning aggregations, their precise location and relative magnitude are not known. The location of the Jeffrey's Ledge spawning, which does support a commercial fishery, was defined by V. Anthony (Northeast Fisheries Center, Woods Hole, MA, pers. comm.). The Scots Bay and southwest Nova Scotia spawning locations were identified from the log records submitted by the Canadian purse-seine fleet. The data sources for timing of spawning for some of the above locations are given by Sinclair and Tremblay (1984).

The historical Grand Manan overwintering area was taken from Huntsman (1953), the Cape Cod and south overwintering area from the results of unpublished research surveys undertaken by the U.S. National Marine Fisheries Service (V. Anthony, pers. comm.), and the Chedabucto Bay – Sydney Bight area from the Canadian purse-seine log records as summarized in Sinclair and Iles (1981) and Sinclair et al. (1981b). The specific location of the Chedabucto Bay overwintering area has been independently verified by research acoustic surveys (Shotton and Randall 1982).

The seasonal distribution of gonad condition was derived from the 1971 port samples collected from the southwest Nova Scotia area. During this year the gonad sampling was the most complete. The data are on file at the Biological Station, St. Andrews, N.B. The juvenile herring distributional area is identified from Anthony (1971) and Sinclair et al. (1981a), both of whom used the catch statistic data from the juvenile fisheries gear components. The expansion and contraction of juvenile range in relation to year-class size differences is documented by Sinclair and Iles (1980). The herring larval distributions were taken from several sources. The Georges Bank and Nantucket Shoals distributions were taken from Lough and Bolz (1979). The distributions associated with the Jeffrey's Ledge and coastal Gulf of Maine spawning locations were taken from Graham (1972, 1982). The larval distributions associated with the Grand Manan, Scots Bay, and southwest Nova Scotia spawning locations were generated from the Bay of Fundy larval survey data set. The details of the survey methodology are given by Sinclair et al. (1979). The mean autumn distributions were generated by averaging the observed values at each sampling station over the 1972–82 period.

Results

Herring Distributions

It is convenient in this synthesis to begin with the adult seasonal migratory stages and to follow on with the early life history larval and juvenile stages to complete the life cycle.

During the summer feeding, adult herring are highly aggregated in only three areas in significant concentrations (Fig. 1A): along the fringes of Georges Bank, off southwest Nova Scotia, and south of Grand Manan Island. The distributions described here and subsequently represent a historical situation prior to collapse of both the Grand Manan and Georges Bank adult herring fisheries. There have been no herring observed on Georges Bank, for example, since the late 1970's; and the Grand Manan spawning stock "collapsed" in the 1870's. In all three areas the predictability of the fisheries from year to year as to area and to time reflects the predictability of the herring seasonal movements and behavior. That these represent (or represented) feeding concentrations is confirmed by the consistent reports by industry of "red-feed" (partly digested zooplankton in distended stomachs) and high levels of fat (up to 25% of body weight). This is stored during the feeding season for use over the winter fasting period. An important behavioral characteristic of herring at this time is their diurnal pattern of vertical migration (Shotton and Randall 1982).

The information on the location, and timing of formation, of the prespawning aggregations is the most detailed for the southwest Nova Scotia spawning group. The herring move closer inshore from the summer-feeding area shown in Fig. 1A at the beginning of August. At this time they suddenly become available to a small vessel drift–gill net fishery that regularly begins operation at this time each year (Sinclair and Iles 1980, 1981). These adult herring are no longer feeding, their fat levels decline, and their gonads ripen rapidly. The duration of the pre-spawning aggregation phase for the herring spawning off southwest Nova Scotia is approximately 2 wk. The drift–gill net catches during the first 2 wk of August (fig. 4 of Sinclair et al. 1979), are interpreted (after discussion with the experienced port samplers) to consist of herring in the prespawning aggregation phase. The precise prespawning aggregations for the other spawning populations in the study area are not well described.

It is inferred that there is a broad range in mean population abundance for the several spawning groups indicated in Fig. 1B (Iles and Sinclair 1982). There are not, however, estimates of each spawning group, but rather for three management units involving stock mixtures (Sinclair et al. 1985). At each of these locations, spawning occurs over a relatively restricted period (a couple of weeks) during the late summer and autumn period (Sinclair and Tremblay 1984). However, consistent differences in the specific timing of spawning between several of the areas within this period are well documented (Sinclair and Tremblay 1984). It is stressed here that there are a number of well-defined spawning areas in contrast with the restricted areas of summer feeding.

Subsequent to spawning the herring migrate to the three overwintering areas: off Cape Breton, southwest of Cape Cod, and historically north of Grand Manan Island (Fig. 1C). At this time, as inferred from observations of the Chedabucto Bay overwintering area, there is restricted movement of the overwintering herring, little or no feeding, and no vertical migration (Shotton and Randall 1982). The duration of this phase in the area off Cape Breton is from the end of November to the end of March. As has been documented for the summer feeding off southwest Nova Scotia there is limited between-year variability in the timing and geographic location of the overwintering distribution.

The migration routes taken from the summer-feeding area to the spawning and overwintering areas are not well described. There is, however, circumstantial evidence suggesting an offshore route for the fish migrating between northeast and southwest Nova Scotia. This includes sonar observations by Canadian groundfish trawlers in Scotian Shelf offshore banks, the historical location of offshore catches on the Shelf (with non-Canadian mobile gear), and the lack of a substantial coastal fishery at the appropriate time of the year in the coastal waters.

The autumn larval distributions subsequent to spawning have been described in considerable detail for several of the spawning areas indicated in Fig. 1B. The most detailed description is that for the Bay of Fundy and its approaches, where standard larval survey with a high station density has been carried out annually since 1972. There has been more than an order of magnitude range in mean larval abundance (Sinclair et al. 1982a), but a relative constancy in the spatial distributions. The highest larval

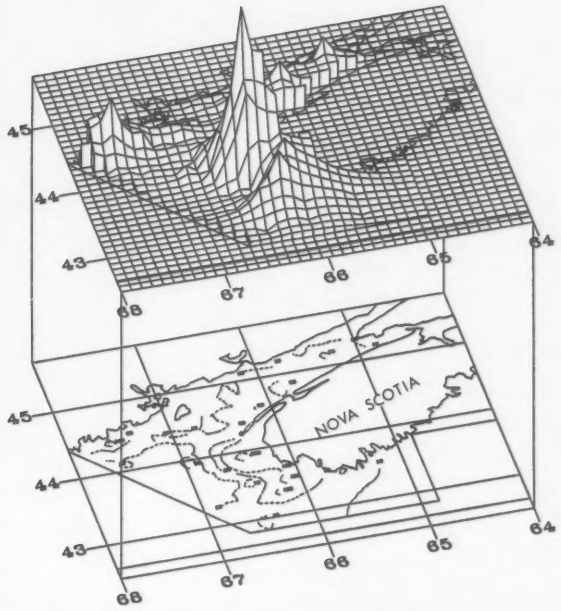

FIG. 2. Autumn larval herring distribution in the Bay of Fundy area.

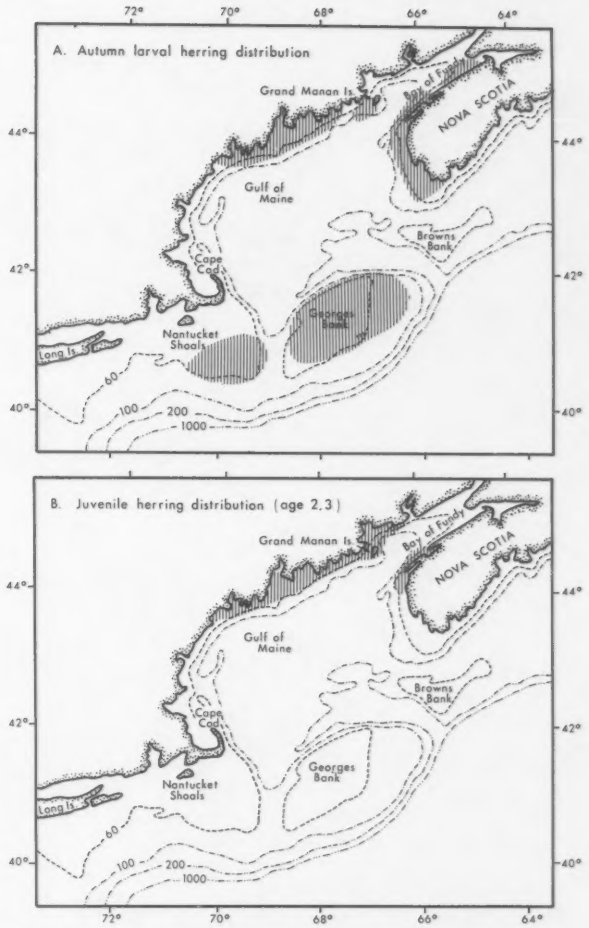

FIG. 3. Larval and juvenile herring distributions in the Gulf of Maine – Scotian Shelf area. (A) Autumn larval distributional areas; (B) juvenile distributional area.

abundance are frequently observed at the mouth of the Bay of Fundy on the Nova Scotia side in close proximity to the spawning location (Fig. 2). A discontinuity in larval abundance exists between this area and that of both Grand Manan and Scots Bay, the two other major spawning areas covered by the survey design. There is a one-to-one relationship between spawning areas and larval distributional areas several months after spawning (Fig. 3A), and thus relatively limited mixing between the progeny of the spawning groups during this phase of the early life history. Larvae from the spawning in Jeffrey's Ledge and Stellwagen Bank may not maintain a discontinuous distribution relative to the coastal Maine spawning populations during the first few months of the larval phase. The life histories of these components are not well described.

The events and distributions during and immediately subsequent to metamorphosis are not well understood. Recently metamorphosed juvenile herring are, however, observed within the Bay of Fundy in close proximity to the larval distributional areas during the summer months (Koeller 1979). In the second and third years, however, the juveniles from all the spawning and larval locations in the study area are believed to be distributed in the coastal embayments of Maine and around the edges of the Bay of Fundy (Fig. 3B). At the time of extremely large year-classes in the juvenile phase, however, there is evidence for an expansion of range up the coast of Nova Scotia. Approximately one third of each year-class recruits to the adult population at age 3, with essentially full maturity reached by age 4 (Sinclair et al. 1979), at which time the year-class migrates with the adult population.

There are several points of interest from the above distributions at various phases of the life history. There are clear, temporally persistent patterns in the spatial distributions at various life history stages. Herring on the Scotian Shelf and in the Gulf of Maine are distributed over very localized areas of the continental shelf. There are or have been three areas of potential importance for summer feeding and overwintering (Fig. 1A and 1C) and a continuous juvenile nursery area, or perhaps two areas if the Bay of Fundy is considered a dividing line (Fig. 3B). In contrast, there are several well-defined spawning locations and larval distributional areas. There is regularity in the timing of events (such as the seasonal migrations to and from summer-feeding and overwintering areas, the formation of the prespawning aggregations, and the timing of spawning) which indicates "programmed" activity. That mixing must be occurring between different spawning stocks at various phases of the life history is evident from the above distributions (three adult summer-feeding and overwintering areas, yet there are a greater number of spawning locations). However, there is evidence for a one-to-one relationship between spawning locations and larval distributional areas. These observations suggest considerable between-spawning population mixing at all phases of the life history except at spawning time itself (by definition) and during the first several months of the larval phase. This life history feature is shared by anadromous species such as Atlantic salmon (*Salmo salar*) and American shad (*Alosa sapidissima*) (Saunders 1981; Dadswell et al. 1983), and to a lesser degree by Atlantic mackerel (*Scomber scombrus*) (Anderson and Pacior-

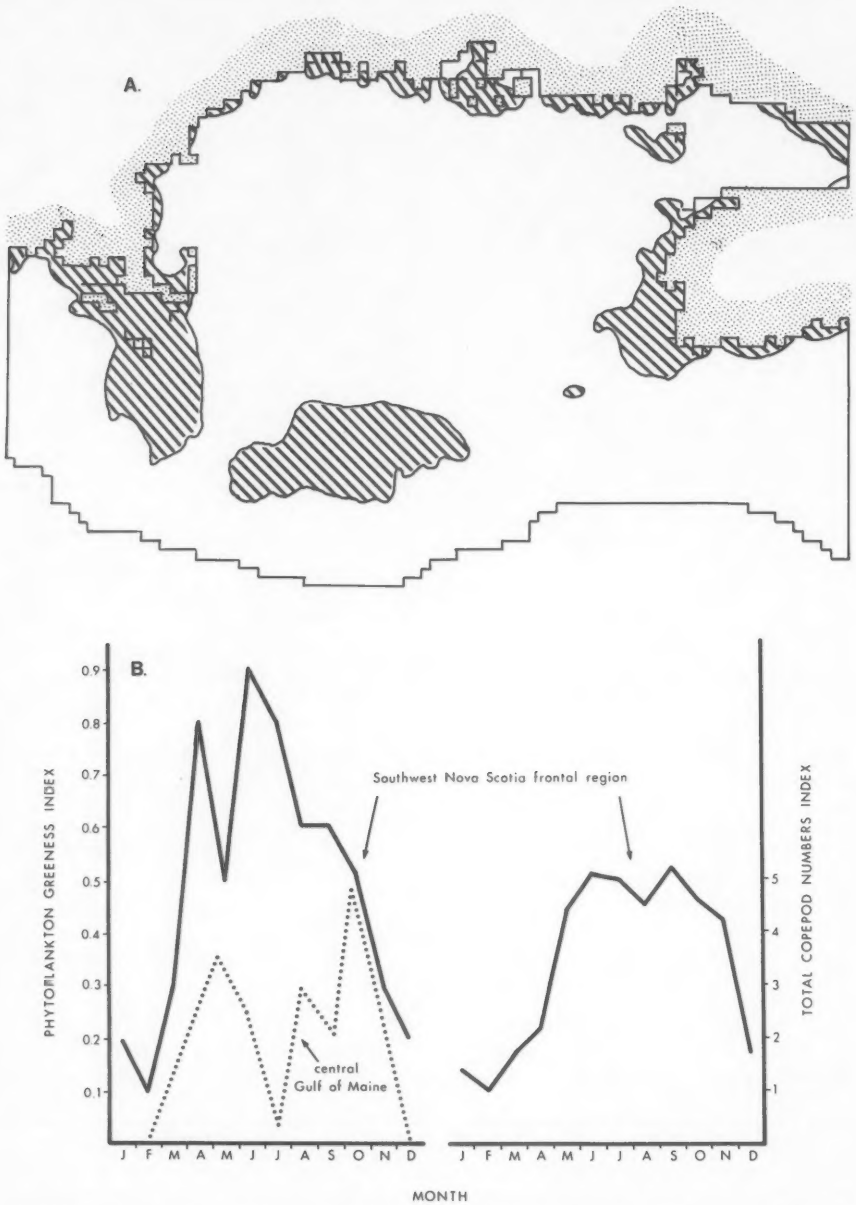

FIG. 4. Oceanographic features in the Gulf of Maine are of importance to herring distributions. (A) Predicted positions of fronts dividing well-mixed from stratified waters (adapted from fig. 6 of Loder and Greenberg 1985). The well-mixed water column is hatched; the remaining area is thermally stratified during the spring to autumn period. (B) Seasonal distribution of an index of phytoplankton biomass and of total copepod abundances in the vicinity of the tidally induced front off southwest Nova Scotia.

kowski 1980) and Atlantic cod (*Gadus morhua*) (Wise 1962) where mixing is inferred to occur respectively at the adult overwintering phase and the summer-feeding phase.

Oceanographic Features

The oceanographic features of several of the above herring distributional areas are well documented. The three areas of adult summer feeding (Fig. 1A) are coincident with predicted tidally induced temperature fronts in the Gulf of Maine (Fig. 4A). In the northeast Atlantic around the British Isles it has been demonstrated that such frontal areas are characterized by high phytoplankton production (Pingree et al. 1975, 1976, 1977). The plankton dynamics associated with the tidally induced features in the Gulf of Maine are less well described. The spatial distribution of phytoplankton production in the frontal area off southwest Nova Scotia during summer cruises is consistent with the northeastern Atlantic results (i.e. high phytoplankton bio-

mass and production in the transition areas between stratified and well-mixed water columns, with lower levels observed both within the stratified and well-mixed areas themselves) (Fournier et al. 1984). Some features of the seasonal plankton distributions in the frontal area can be derived from the Continuous Plankton Recorder (CPR) data. From 1961 to 1974, CPR data have been collected on a near monthly basis following a commercial shipping route between Boston and Halifax. The part of the cruise track that traverses the summer-feeding area was selected for analysis. Since there are always gaps in the monthly time series for any one year, the monthly estimates of relative plankton biomass were averaged using all years. The seasonal distribution of phytoplankton biomass (as estimated by a greeness index) and total copepods at the frontal area are shown in Fig. 4B. It can be inferred that this area, and the other two adult herring summer-feeding areas (Fig. 1A), are characterized by continuous high primary and secondary production through the spring to autumn months (the phytoplankton biomass seasonal distribution for the thermally stratified central Gulf of Maine area is shown for comparison). Interestingly, the adult summer-feeding herring off southwest Nova Scotia leave the feeding area (in the July–September period, depending on the spawning component) when food, as estimated by total copepods, is still abundant.

The autumn larval distributions described in Fig. 3A are roughly coincident with the predicted well-mixed areas shown in Fig. 4A. It is observed that the larval populations are distributed for several months in these geographically predictable high-energy locations in spite of the residual circulation. Estimates of residual currents based on drift bottle recoveries off southwest Nova Scotia within the larval distributional area suggest that larvae in the upper layer of the water column would be advected (either into the Bay of Fundy or across the mouth of the Bay toward Maine) at about 5–10 km a day if they were drifting passively (R. W. Trites, Bedford Institute of Oceanography, Dartmouth, N.S., pers. comm.). Thus, during the first 3 mo of the larval phase a displacement of several hundred kilometres would be expected. Displacement on this scale is not, however, observed (compare spawning locations in Fig. 1B with larval distributions in Fig. 2 and 3A). In the spring (March–April), about 7 mo after spawning, the discontinuities within the Bay of Fundy area are not clear, and the overall distribution has shifted further into the Bay in the direction of the residual currents (unpubl. data). Thus, discreteness between spawning areas is observed during the first several months of the early life history, but not necessarily for the complete larval/postlarval phase. From detailed studies of herring larvae in estuaries, it is inferred that for such areas larval retention during the first several months is achieved by the interaction between vertical migration in relation to the tidal currents (Fortier and Leggett 1983; Graham 1972). Comparable studies on vertical migration have not been undertaken in shelf waters.

Larvae from the various late-summer to autumn spawning populations in the Gulf of Maine area spend up to 7 or 8 mo in the larval phase (Sinclair and Tremblay 1984). The average growth rate over this period is low compared with that of spring-spawned larvae that grow large enough to metamorphose in a few months (Sinclair and Tremblay 1984). The feeding environments of the larval distributional areas are therefore of interest. Recent larval herring surveys of the Bay of Fundy and its approaches included estimates of zooplankton biomasses (Fig. 5). During late summer and autumn the larval distributional areas (Fig. 3A) coincided with areas of relatively low

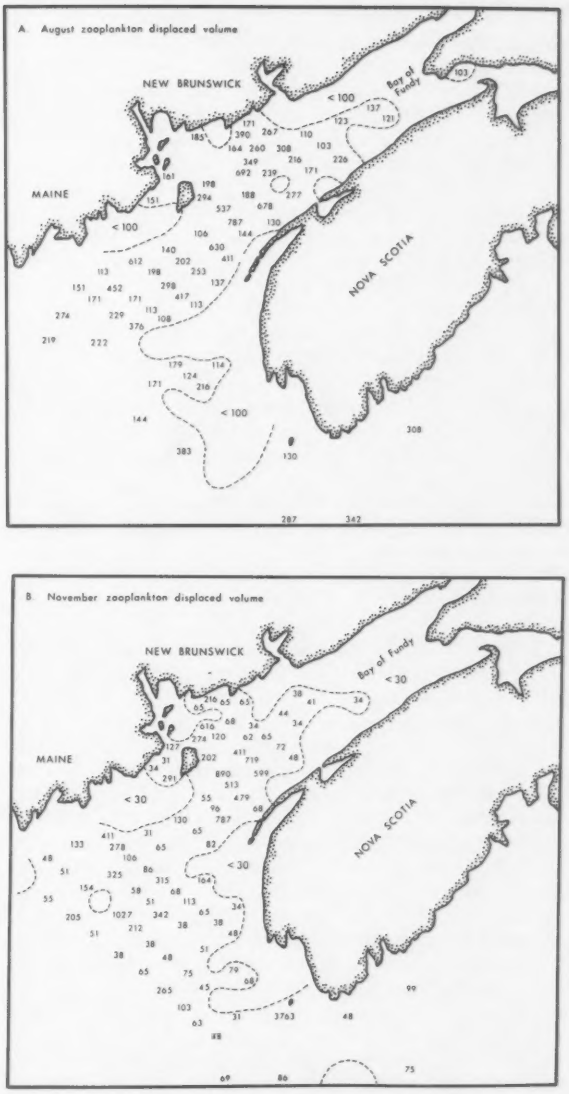

FIG. 5. Distribution of zooplankton-displaced volume in the Bay of Fundy area during (A) August and (B) November.

zooplankton biomass. Moreover, the biomass in November during the early growth period for the larvae was, perhaps expectedly, lower than in the summer period.

The paradox of the life history strategy is that larval from several of the spawning populations in the Gulf of Maine area (southwest Nova Scotia, Scots Bay, and Grand Manan) occur in tidally energetic areas of relatively low food availability at a time of year when temperature is also lowest. A hypothesis to account for the timing of spawning of herring and the duration of the larval phase deals with this paradox (Sinclair and Tremblay 1984). The hypothesis involves two contraints. First, the larvae of a discrete herring population develop within, and thus are adapted to, the specific oceanographic conditions of their larval retention area. Second, metamorphosis from the larval to juvenile form occurs primarily within a restricted period of

the year (April–October). Given these two constraints, it is hypothesized that the timing of spawning of a herring population is a function of the time necessary to complete the larval phase and yet metamorphose within the acceptable seasonal envelope. Populations with larval retention areas that are not conducive to rapid growth have to spawn in the autumn period to satisfy the above constraints. Even though the Georges Bank larval distributional area is generally considered to be highly productive, there is some evidence indicating lower zooplankton biomass within the well-mixed area over the Bank. Taking Georges Bank as a whole, zooplankton production is not high for a temperate shelf environment, being equal to the Scotian Shelf and two-thirds that of the Gulf of Maine (Cohen et al. 1982). Moreover, transects across Georges Bank indicate that copepod biomass is considerably lower in the central mixed area (Dagg and Turner 1982). High secondary production estimates may be restricted to the frontal areas proper, at the edges of the Bank. The water mass over the central part of the Bank itself, where the bulk of the larval herring population is "retained," is perhaps not as productive in zooplankton as generally perceived. For several of the spawning groups at least (Fig. 5), it is suggested then that the larval distributional areas are not rich in terms of larval food.

Discussion

In an earlier synthesis on Atlantic herring stocks we hypothesized that the number of herring stocks and the geographic location of their respective spawning sites are determined by the number, location, and extent of geographically stable (or predictable) larval retention areas (Iles and Sinclair 1982). If the stock hypothesis proves robust, much of the herring distributional information presented for the Gulf of Maine – Scotian Shelf area is readily interpretable. The locations of spawning and of the larval distributions are a function of the location of the physical features associated with "larval retention." This latter term has been occasionally misinterpreted. It is not inferred that the larvae are retained passively by the circulation features of the larval distributional area, but rather by an active behavioral response to the physical regime. Neither is it inferred that the larval distributional area is static. Scale is important. individual larvae must indeed drift horizontally during their vertical migrations, but nevertheless the populations are observed to maintain a discrete distribution in a relatively fixed geographic location for several months. The observed displacements in the larval distributional areas, although in the direction of the residual current, are not on the same scale as the water mass displacements.

That there is homing of mature adults to the larval retention areas for spawning can be deduced from the particular features of the Isle Verte herring population in the St. Lawrence estuary (see Auger and Powles 1980, Henri et al. 1985 for distributional information). Herring of this spawning population are particularly small at each age-class compared with other herring in the Gulf of St. Lawrence. Because of this they are frequently called "pygmy" herring. Only pygmy herring spawn off Isle Verte in the estuary in the late spring, but these smaller herring are caught on the Magdalen Shallows in the Gulf of St. Lawrence during the feeding part of their annual migration. They can be readily identified from the unusual morphology of their otoliths. The larval phase of this population is exceptionally long, in that the larvae from the "spring" spawning event are interpreted to overwinter in this phase (10–11 mo duration of larval phase) (Sinclair and Tremblay 1984). The exceptionally slow larval growth in the upper St. Lawrence estuary is interpreted here to be the cause of the unusual morphology of the otolith. Thus, the link from the larvae growing within a very poor retention area, to homing of the adults to this same precise geographic location to spawn, is interpreted here to be marked on the otolith. Within the Gulf of Maine area, homing to the diverse spawning areas is inferred to occur, but this phenomenon cannot be directly shown.

The adult summer-feeding areas in the Gulf of Maine area are associated with the location of tidally induced temperature fronts (compare Fig. 1A with Fig. 4A) where plankton production is high. The underlying reasons for the specific location of the overwintering areas (which can be at considerable distances from other parts of the adult distribution) and of the juvenile nursery area are, however, still not obviously determined. We note that overwintering areas, where the herring activity appears to be considerably reduced, are characterized by slow currents relative to the Gulf of Maine area, so that they might be considered low-energy refuge areas.

To a large degree, then, the herring problems addressed by Hjort (1919) during the Canadian Fisheries Expedition in 1914–15 may be resolved. The results described above, and their interpretation, however, are inconsistent with some fisheries biology theories. First, it can be inferred that larval retention areas in the study area are occupied in spite of their particular plankton characteristics rather than because of them as advocated, for example, by Cushing (1975) and Lasker (1975). The criterion is that maintenance of a reproductive unit is possible, not that conditions are optimal. Following this interpretation, everything else related to the early life history can be considered secondary. Bottom type for spawning, larval food, predators on larvae, temperatures, etc., all vary greatly for different herring stocks. Second, the results suggest that migration to the juvenile nursery areas occurs subsequent to metamorphosis rather than during larval drift, which is inconsistent with the general theory of fish migration (Harden-Jones 1968). This point has also been suggested for groundfish species on the Scotian Shelf (O'Boyle et al. 1984). Third, the observation of mixing at all stages of the life cycle except spawning itself and during the first several months of the larval phase, in conjunction with the indication that population sizes for the respective spawning stocks are defined by the size of the hydrographic feature involved in larval retention (Iles and Sinclair 1982), infers that interactions at the between-population mixed phases have little influence on fitness. This implies that intraspecific competition at the adult phase is not of significance. There is little evidence of density-dependent growth in adult Atlantic and Pacific herring. In fact, in two geographic areas a positive relationship between population size and growth rate over a large range in population size has been described (Haist and Stocker 1985; Sinclair et al. 1982b). Individual juveniles and adults sharing identical environmental influences can contribute to gene pools differing in size by several orders of magnitude, and to populations that are at the same time either at the high or low end of their abundance ranges.

If this interpretation of the empirical observations is correct, it is of interest to speculate on why, in an evolutionary sense, the existence of a geographically predictable larval retention area is the necessary condition for the establishment (and limitation of absolute abundance) of herring populations. Maintenence of an aggregated larval population may be essential for the successful establishment of a viable reproductive unit (a spawning stock).

Larvae lost from the aggregate (or from spawning in an area where the larval population drifts and individuals are dispersed) quite simply may not be able to recruit to the migrating populations subsequent to metamorphosis. The geographical predictability requirement of the hydrographic features necessary for the establishment of a viable population is plausibly linked to the bottom-spawning behavior of herring (i.e. the eggs are attached to the bottom in relation to a geographically reproducible hydrographic feature). The adaptive value of homing of adult herring to spawn in their place of hatching is interpretable: from a larvae's point of view, homing permits the maintenance of a temporally persistent larval population in a fixed geographical location.

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Stock Assessment Problems in Atlantic Herring (*Clupea harengus*) in the Northwest Atlantic

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Total annual catches of Atlantic herring (*Clupea harengus*) in NAFO statistical areas 3–6 have declined steadily since 1968, and have not rebounded after management measures were implemented in the late 1970's (unlike demersal species in the area). The accuracy of the biomass estimates generated by sequential population analysis is evaluated by a retrospective analysis for 3 of the 10 management units for herring fisheries. In each case, the stock assessments have tended to seriously underestimate the declines in stock abundance and overestimate the upswings. Fishing mortalities have exceeded $F_{0.1}$, but they have rarely exceeded F_{max}, the level below which growth overfishing is prevented. Three assumptions in the stock assessment process are evaluated in relation to the 4WX management unit: (1) the various management units are in fact self-sustaining populations; (2) catchability (i.e. fishing mortality per unit of effort) is constant and independent of stock size; and (3) the population is in the stable age distribution. We conclude that at least part of the management failures are due to invalid assumptions in the stock assessment models. An approach that has prevented growth overfishing may well have caused recruitment overfishing. Atlantic herring should be managed on principles suited to salmon rather than those applied to groundfish.

Les prises annuelles totales de hareng de l'Atlantique (*Clupea harengus*) dans les zones statistiques 3 à 6 de l'OPANO diminuent régulièrement depuis 1968 et n'ont pas remonté après l'application de mesures de gestion à la fin des années 1970 (contrairement aux espèces démersales de cette région). À l'aide d'une analyse rétrospective de 3 des 10 unités gestionnelles de la pêche du hareng, les auteurs évaluent la précision des estimations de biomasse découlant d'une analyse de population séquentielle. Dans chaque cas, les évaluations de stock ont eu tendance à sérieusement sous-estimer les déclins des stocks et à surestimer les améliorations. La mortalité par pêche a dépassé $F_{0,1}$, mais a rarement dépassé F_{max}, le niveaux au-dessous duquel la surpêche des classes de petite taille est évitée. Trois hypothèses liées au processus d'évaluation des stocks sont examinées en rapport avec l'unité gestionnelle 4WX : (1) les diverses unités de gestion représentent en fait des populations autonomes ; (2) la capturabilité (c.-à-d. la mortalité par pêche par unité d'effort) est constante et indépendante de la taille du stock ; et (3) la distribution des âges dans la population est stable. Les auteurs formulent la conclusion qu'une partie au moins des échecs de la gestion est le résultat d'hypothèses invalides dans les modèles d'évaluation des stocks. Il se peut qu'une approche ayant empêché la surexploitation des classes de petite taille ait causé une surpêche du stock reproducteur. Le hareng de l'Atlantique devrait être géré d'après des principes qui conviennent au saumon plutôt que selon les principes appliqués aux poissons démersaux.

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The fisheries record in the eastern Atlantic up to the late 1970's had demonstrated a difference in the severity of declines between demersal and pelagic fisheries. In addition, the response of fish stocks to the relatively strict management measures applied in the northwestern Atlantic since the mid-1970's has been qualitatively different between demersal and pelagic species. These differences, apparently representing differences in their resilience to exploitation, as the

populations respond to changes in fishing mortality, have raised questions whether fisheries management models that are appropriate for groundfish are suitable also for pelagics. The aspects of the population biology of pelagic species that might account for their greater susceptibility to excessive fishing pressure were considered by the Aberdeen Symposium in 1978 (Saville 1980a). Conclusions were as follows (Saville 1980b):

(1) Catchability (q) of pelagic fish increases as population size decreases. This factor results in maintenance of high catch rates at low abundance, and effectively prevents much of a natural economic brake in the years just prior to pelagic fishery collapses.

(2) The production/biomass ratio for pelagic fish species is lower than for demersal species.

(3) There is, possibly, a shallower ascending limit of the stock–recruitment relationship in pelagic species than is the case for demersal species.

(4) As population size of pelagic species decreases, and if the predator population remains relatively constant, natural mortality will increase. This effect, however, is not restricted to, or characteristic of, pelagic species alone.

Evidence for changes in the catchability coefficient was strong, but the other conclusions were less well supported by evidence presented at the Symposium. The Symposium did not reach conclusions concerning the differential applicability of the management models to the two species types, and made no recommendations for different management approaches.

Six years have elapsed since the Aberdeen synthesis, and information on individual herring stocks and fisheries has accumulated that warrants an update of the situation. This paper deals with events in the northwestern Atlantic and addresses three issues. The first concerns the management of Atlantic herring (*Clupea harengus*) in the northwestern Atlantic. The assessment record is critically evaluated with the aim of determining as objectively as possible how accurate the estimates of herring abundance have been. Secondly, the logical sequence of steps in the analytical assessment procedure are described, and some key assumptions identified. The importance of those assumptions are discussed in relation to the Gulf of Maine – Scotian Shelf herring complex. Finally, conclusions are drawn that amplify the list drawn up by Saville (1980b) and enumerated above. This leads to the recommendation of a different management approach which recognizes the particular biological features of herring.

Stock Assessment Record for Atlantic Herring in the Northwest Atlantic

Prior to the early 1960's there was a relatively stable annual herring catch somewhat in excess of 300 000 t in NAFO statistical areas 3–6 (Fig. 1). With the introduction of mobile gear in the 1960's by both coastal states (Canada and United States) and foreign fleets that exploited segregated and mixed stock concentrations, the catches quickly climbed to almost 1 million t in 1968. There has been a steady decline since then, with the 1982 catch being close to 200 000 t. This decline affected different stocks to different degrees, and some spawning populations have been reduced to near extinction. The small Grand Manan spawning population had collapsed during the late nineteenth century apparently as a result of overfishing at the susceptible overwintering phase (the evidence is provided by Huntsman 1953). In the 1970's the very large Georges Bank and the substantial Gulf of St. Lawrence Magdalen Island

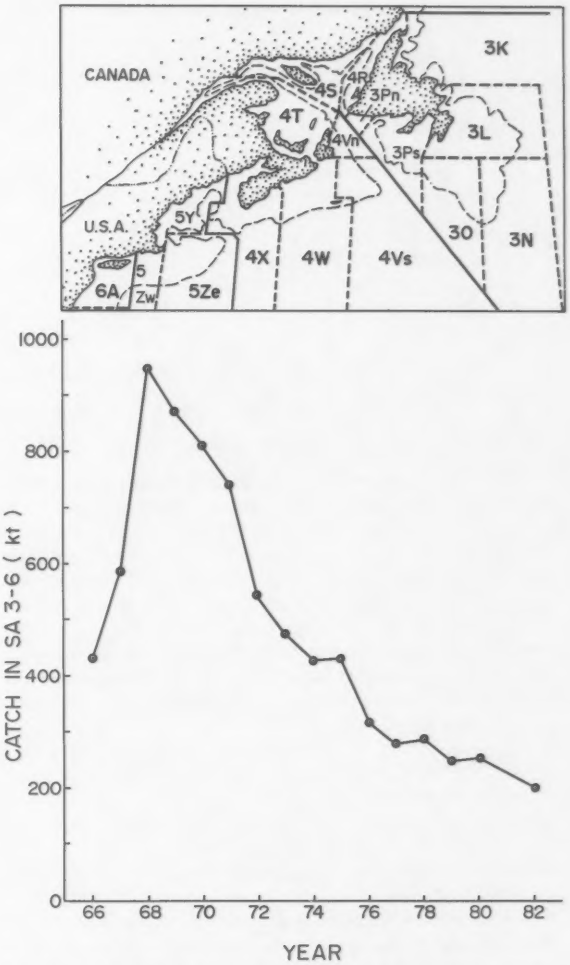

FIG. 1. Total catch of Atlantic herring from 1966 to 1982 in NAFO statistical areas 3–6. The NAFO statistical system is shown in the inset.

spawning populations have been virtually eliminated (see respectively Anthony and Waring 1980 and Cleary and Worgan 1981). In summary, present annual catches of Atlantic herring are considerably less even than the long-term average prior to the 1960's, and are taken from a reduced number of spawning populations with considerably more effort.

Total allowable catches (TAC's), as a direct control of removals, were not set on herring in the western Atlantic until 1972, and coastal state jurisdiction of this resource along with stricter regulations did not occur until 1977. Thus, the initial dramatic decline in catches and population abundances took place in the absence of management control. However, the implementation of TAC's in the early 1970's has not had any obvious effect, other than a decline in the rate of decrease, on the herring catches (and by implication the herring populations). These have not rebounded to earlier levels as has been the case for certain demersal species (cod and haddock on the Scotian Shelf for example (Sinclair et al. 1984)). Both demersal and herring stocks had been heavily exploited prior to implementation of TAC's, and there is no reason to conclude that the

TABLE 1. Management units in the northwest Atlantic.

East coast Newfoundland (3KL)
Fortune Bay (3Ps)
St. Mary's – Placentia Bay (3Ps)
West coast Newfoundland (4R)
Northern Gulf of St. Lawrence (4S)
Southern Gulf of St. Lawrence (3Pn and 4T)
Sydney Bight (4Vn)
Scotian Shelf (4WX)
Gulf of Maine (5Y)
Georges Bank and south (5Z and 6)

enforcement of the regulations was differentially applied to the two species categories.

Stock Assessments, 1977–82: A Backward Look

The accuracy of the stock assessments during the postextension of jurisdiction period (1977–82) is evaluated for representative selected management units. The herring fisheries in the northwestern Atlantic are divided into 10 management units (Table 1) of which 3 are evaluated (Scotian Shelf, southern Gulf of St. Lawrence, and Fortune Bay in Newfoundland). In the present analysis the accuracy of the annual stock assessments are evaluated retrospectively using the subsequent assessments. This approach takes advantage of the self-correcting property of sequential population analysis (SPA) (Pope 1972). For example, the estimate of 1977 stock size from SPA is very much a best guess in 1977, but by 1983 using the same methodology we have a good fix on what the 1977 stock size actually was. Thus, the recent assessments can be used to evaluate the accuracy of the earlier assessments. The relevant stock assessments for the three management units are identified in Table 2. For each unit and year the adult biomass (age 4 and older) was taken from the appropriate assessment (or estimated from data presented there). The weight-at-age data used to derive the biomass estimates are given in Table 3. Natural mortality has been assumed to be 0.2 for all the herring assessments. It should be noted that since a single set of mean weights-at-age is used for estimation of biomass for all years, the biomass estimates are not identical to those reported in the assessments.

The 1977 biomass estimate for 4WX adult herring in the 1978 stock assessment (i.e. using data up to 1977) was 551 000 t (Table 4). The 1983 assessment indicates, however, that the revised value is about 288 000 t; the 1978 assessment overestimated stock size of the most recent year by about 90%, and the quota derived by applying the management strategy fishing mortality (in this case, $F_{0.1}$ from the analytical yield model) to the stock size was too high by the same margin.

The 1978 biomass estimate for southern Gulf of St. Lawrence (4T) herring in the 1979 stock assessment was 361 000 t (Table 4). The 1982 assessment indicates that the correct value was closer to 52 000 t, an overestimate of almost 600%. Again, the overestimate obviously generated an unrealistic quota in relation to management objectives. The quotas in fact were so high during this period in which the stock size was grossly overestimated that they were never reached. The Fortune Bay retrospective analysis (Table 4) indicates a somewhat smaller overestimate in the most recent year of the 1978 assessment (50%). The difference between the adult biomass estimates of the various stock assessments are summarized in Fig. 2a–2c. The important point is that in almost all the cases evaluated, the errors are positive (i.e. overestimation of herring abundance). Note that not all of the annual assessments for the three management units are significantly biased; the worst-case examples have been pointed out here.

Quotas have been established for these management units in relation to $F_{0.1}$ exploitation levels, or lower than $F_{0.1}$ in the southern Gulf of St. Lawrence herring in order to rebuild spawning stock size. Although estimated fishing mortalities (Fig. 3) have exceeded $F_{0.1}$, the estimates are not particularly high compared with the fishing mortalities exerted on North Sea demersal stocks, for example (Daan 1978). The overshoot in fishing mortality relative to the $F_{0.1}$ target has been due to a combination of overestimates in stock size and a lack of enforcement of the quotas implemented. The adult fishing mortalities have rarely exceeded F_{max}, the level below which growth overfishing is prevented (Cushing 1975). Thus, there is somewhat of a paradox here; even at relatively moderate exploitation rates, stock sizes have declined continually and spawning stock units have been fished to commercial extinction. This "paradox" is addressed in the following sections.

We conclude from the above examples that the stock assessment biologists have tended to overestimate stock size. The critical question, then, is what is causing the inaccuracies in the Atlantic herring stock assessment? This question is addressed by a more detailed evaluation of the herring complex in the Gulf of Maine area and in particular the 4WX assessments.

Steps in an Analytical Stock Assessment

An "analytical" assessment for a fishery that has been sampled to provide the age composition of the catch can conveniently be divided into four steps:

(1) Definition of the management unit itself (i.e. what catch is to be included in the analysis, and more specifically in the catch-at-age matrix). Quite naturally, management units are usually defined in the early stages of the development of the management regime and tend not to be reviewed at frequent intervals. The often unstated, but critical, assumption is that the management unit represents a population that responds as a unit to changes in abundance by feedback mechanisms. Every herring in the management unit is assumed to be equal in its ability to contribute to population growth, or to its decline.

(2) Estimation of "population" size including the abundance of the recruiting year-classes within the management unit using SPA. Effort and catch per unit of effort (CPUE) from mobile gear components of the fishery have often been used in the iterative procedure of selecting the input fishing mortalities for the most recent year of the analysis. These selected values largely determine the estimate of the current size of the population. This procedure assumes that catchability (q) is constant over the time period and abundance range for which there are effort data.

(3) Estimation of the appropriate fishing mortality in relation to the management strategy, using an analytical yield model. For example, the Beverton–Holt derivation of the model can be used to generate F_{max} or $F_{0.1}$ for the expected selectivity-at-age vector of the combined gear components of the management unit. The use of the analytical yield model to generate the desired F levels assumes that the population is in the stable age distribution.

TABLE 2. Stock assessments evaluated in the retrospective analyses.

Management unit	Year of assessment	Comments on analysis	Reference
4WX	1977		Miller and Stobo 1977
4WX	1978	Recalculated using $F = 0.3$	Stobo et al. 1978
4WX	1979	Estimated using adjusted effort	Sinclair et al. 1979
4WX	1980	Estimated population no. for stock option 1	Sinclair and Iles 1980
4WX	1981	Population nos. (option B)	Sinclair and Iles 1981a
4WX	1982	No reanalysis done	Sinclair et al. 1982
4WX	1983	No reanalysis done	Iles and Simon 1983
4T	1978	—	Winters 1978
4T	1979	—	Winters and Moores 1979
4T	1980	—	Winters and Moores 1980a
4T	1981	—	Cleary 1981
4T	1982	—	Cleary 1982
Fortune	1977	—	Winters and Moores 1977
Fortune	1978	—	Winters and Moores 1978
Fortune	1979	—	Moores and Winters 1979
Fortune	1980	—	Winters and Moores 1980b
Fortune	1981	—	Moores et al. 1981

TABLE 3. Weight-at-age vectors used to generate estimates of population biomass. (Sources: 4WX, Sinclair and Iles (1981a); 4T, Winters and Moores (1980a); Fortune Bay, Winters and Moores (1977)).

Management unit	Age	Mean weight (g)
4WX	4	172
	5	218
	6	254
	7	286
	8	323
	9	354
	10	389
4T	4	178
	5	216
	6	241
	7	269
	8	288
	9	300
	10	314
Fortune Bay	4	206
	5	240
	6	276
	7	310
	8	335
	9	345
	10	360

(4) The management strategy fishing mortality generated by step 3 and corrected for the selectivity-at-age for the combined fishing gears is applied to the vector of abundances-at-age for the most recent year generated by step 2 to project the TAC.

Three of the assumptions of the assessment procedure used in the western Atlantic are critically examined: (1) the management unit represents a population; (2) q is constant; and (3) the "population" is in the stable age distribution. The area under consideration is the Gulf of Maine and the Scotian Shelf, and the management unit chosen is that of NAFO subdivisions 4WX.

A Critical Review of the Assumptions in the 4WX Herring Assessment

Even though the management units were initially defined within ICNAF in relation to the best biological advice available at the time, the 4WX Atlantic herring management unit is clearly not a population in any definable ecological sense. The various components of the fishery that are included within the unit are shown geographically and temporally in Fig. 4. The management unit is defined in relation to the statistical areas defined by NAFO, in this case those herring fished in 4WX. The herring, however, do not respect such arbitrary lines. The life history and migrations of herring in the Gulf of Maine – Scotian Shelf area are described in detail by Sinclair and Iles (1985). Only the pertinent aspects are summarized briefly here.

Summer feeding of adults occurred in recent decades principally in two quite restricted areas: on the shelf in the vicinity of the tidally induced temperature fronts off southwest Nova Scotia and, until the collapse of the Georges Bank fishery, around the perimeter of the Bank. In late summer, herring from these two areas segregate and migrate to their respective spawning areas which include Scots Bay, southwest Nova Scotia itself, Grand Manan, Jeffrey's Ledge, northeast Georges Bank, Nantucket Shoals, and coastal Maine (three separate spawning groups having been proposed in this latter area). After spawning in the late summer to autumn depending on the specific spawning site, the herring migrate and reaggregate in two overwintering areas. These are in the Chedabucto Bay area to the northeast and to the southwest of Cape Cod close to shore. The progeny of these diverse spawning populations are distributed as juveniles from the coast of Maine into the Bay of Fundy and along the coast of southwest Nova Scotia. At any one time there may be discontinuities in the distribution of juveniles, but these boundaries are not necessarily constant from season to season or from year to year. Over half a million fish have been tagged in this area, the tag returns demonstrate extensive and regular seasonal and life history migrations as well as considerable between-population mixing (Stobo 1983).

The conclusion of interest in this review, then, is that there is considerable mixing between populations at all stages of the life

TABLE 4. Estimates of population biomass (age 4+) in kt for the 4WX, 4T, and Fortune Bay management site.

Assessment	Year																	
	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
4WX																		
1977	—	—	523	534	502	478	319	220	161	510	449	410						
1978	336	408	523	539	505	481	319	223	170	571	523	505	551					
1979	354	439	569	586	553	528	361	254	188	538	466	414	384	245				
1980	337	410	527	541	506	481	318	221	164	504	430	366	314	179	106			
1981	343	418	537	551	510	481	319	220	163	495	419	356	301	169	104	439		
1982	338	412	530	544	504	475	314	216	159	484	406	340	285	154	95	407	356	
1983	341	416	534	548	516	480	317	219	160	488	411	343	288	156	92	355	310	219
4T																		
1978	—	—	—	—	1125	684	461	333	260	220	182	161	157					
1979	—	—	—	—	1117	700	475	346	257	242	209	188	214	361				
1980	—	—	—	—	1213	742	514	380	292	247	209	186	189	304	295			
1981	—	—	—	—	1014	584	396	257	179	138	108	74	59	77	54	26		
1982	—	—	—	—	989	616	401	272	184	142	111	77	63	52	59	33	36	
Fortune Bay																		
1977	—	8	44	35	20	29	24	21	10	5	4	4						
1978	—	—	—	—	20	29	24	22	8	7	5	4	3					
1979	—	9	43	34	19	27	23	19	8	4	2	2	1	6				
1980	—	8	43	34	19	27	23	19	7	4	2	2	1	4	3			
1981	—	—	—	—	19	27	23	19	7	4	2	2	1	4	3	2		

history except for the spawning period itself and the first several months of the larval stage (Sinclair and Iles 198lb; Iles and Sinclair 1982). In addition, there is strong evidence to show that herring spawning outside 4WX migrate into the management area. The evidence is less clear that herring spawning in 4WX migrate outside the management area. Two examples are given.

Two major tagging experiments were carried out on the adult summer feeding and spawning grounds off southwest Nova Scotia (Stobo 1983). The aim was to tag the herring in the ripe-and-running stage during active spawning. In the first experiment 60% of the long-distance returns came from the overwintering area to the northeast, predominantly within subarea 4W, and 40% came from areas to the southwest in subareas 5 and 6. In the second experiment, which was more successful in matching the spawning event proper, the split was 80% to the northeast and 20% to the southwest. The interpretation given to these results is the following. The first experiment tagged the mixed population feeding aggregations which subsequently segregate in their migration to spawning areas, and overwinter in both directions. The second experiment tagged predominantly southwest Nova Scotia spawning fish, most of which overwinter in subarea 4W.

The second example of between-population mixing deals with the juvenile herring fishery in the Passamaquoddy Bay area (4X). An analysis of the summer growth of age 2 herring in the Bay indicates a shift in the relationship between length increment and initial length coincident with the collapse of the Georges Bank adult fishery (Sinclair et al. 1981, fig. 5). The interpretation given is that the Georges Bank juveniles (NAFO subdivision 5Ze) were distributed up into the Bay of Fundy in 4X, mixed in with the juveniles from other spawning populations of the Gulf of Maine area. The elimination of this major source of juveniles is interpreted to have generated the observed growth characteristic changes.

In summary, the 4WX management unit includes several spawning populations (southwest Nova Scotia, Grand Manan, Scots Bay, and other small local populations), as well as mixed aggregations of juveniles and summer-feeding fish comprising herring from the Gulf of Maine area as a whole. The population complexity of this particular management unit is likely typical and not exceptional. If so, there is in general great difficulty in matching geographically defined management units to self-sustaining but highly migratory "interwoven" populations.

The second assumption identified is that the catchability coefficient, q, is constant. Again, this assumption has been examined for the 4WX management unit. In the earlier assessments the purse-seine summer-feeding and overwintering fishery catch rates were used to provide input F values to the SPA. From discussions with the purse seiners it was clear that both the individual fisherman was "learning" each year and that the fleet was operating more as a unit. This suggested that assessments should take into account changes in q. On the basis of a questionnaire circulated to a subset of the purse-seine captains, Sinclair et al. (1979) inferred somewhat arbitrarily that q was increasing steadily, and that the catch rates should therefore be adjusted downward by 10% per year. In the following two assessments the year-to-year changes in q were estimated quantitatively (Sinclair and Iles 1980, 1981a). A population matrix was generated for the combined 4WX fishery using the best estimate for the starting fishing mortality vector. This could be combined with the catch matrix for the summer purse-seine fishery alone (which accounted for, on average, 50% of the total annual catch), using the Baranov (1918) catch equation to generate a fishing mortality matrix for the summer purse-seine fishery alone, for each of a series of years. Given the total fishing effort for those years, this leads to an estimate of the annual mean for q. The results for the purse-seine gear component (Fig. 5a) indicate a threefold increase in q for this fishery. This increase coincided with the sharp decrease in the fishable biomass of herring in the population, which is consistent with Pope's (1980) conclusion drawn for other schooling pelagic fisheries. The relationship between fishable biomass and

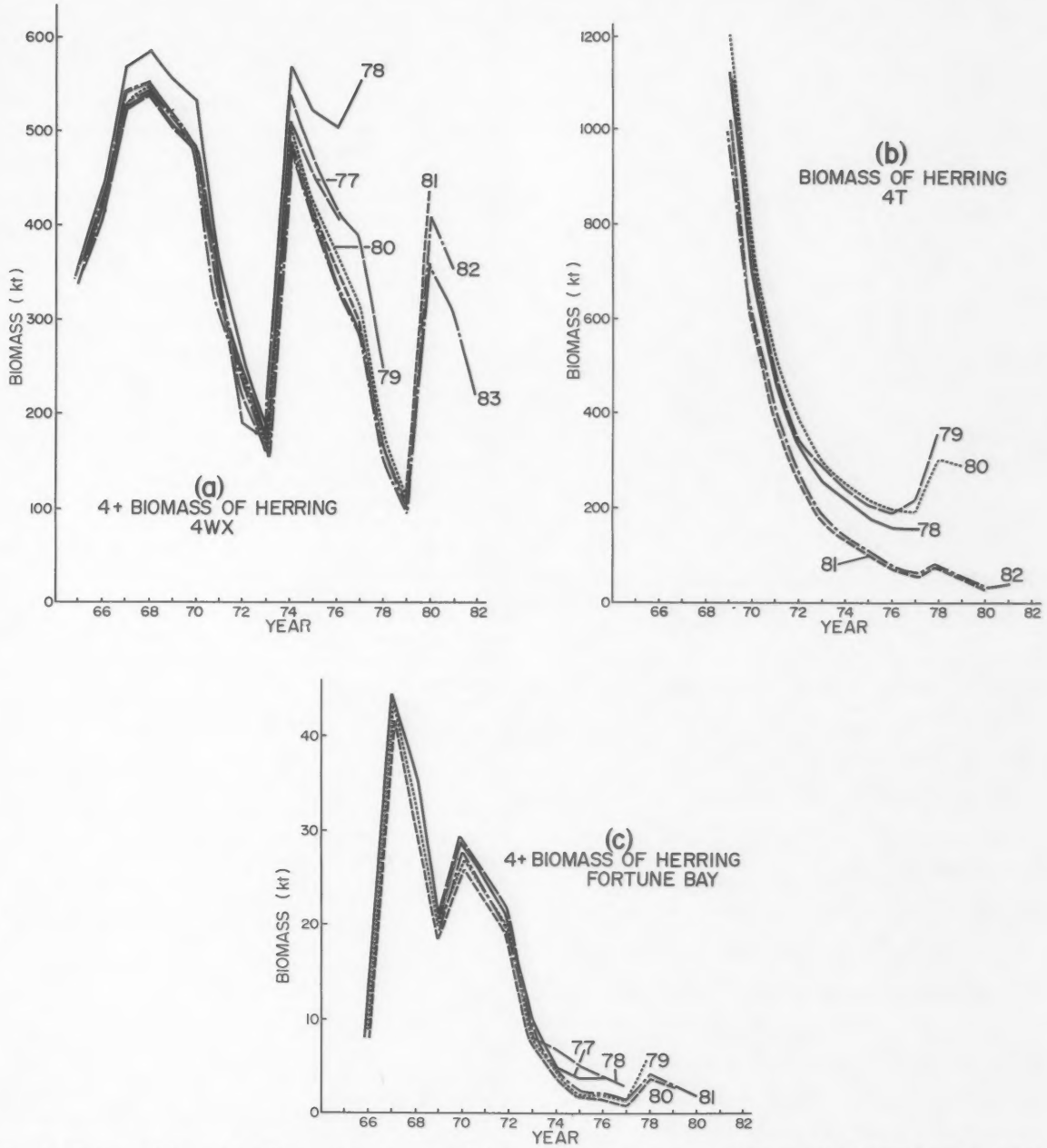

FIG. 2. Estimates of the age 4 and older population biomass made during different stock assessments (1977–83) of the (a) 4WX management unit, (b) southern Gulf of St. Lawrence management unit, and (c) Fortune Bay management unit.

unadjusted CPUE (i.e. uncorrected for trends in q) for the summer purse-seine fishery is shown in Fig. 5b. The steep declines in biomass are not reflected in comparable catch rate decreases. For example, a fishable biomass of 700 000 t in 1969 generated a CPUE of 40 t/set. The same catch rate was observed 10 yr later in 1978 at a fishable biomass of less than 300 000 t.

There is some circularity in the method used here to estimate q trends, in that the catch matrix for the gear component being evaluated is used twice, both to estimate the total "population numbers" and then to estimate the fishing mortality for the specific gear component. In spite of the limitations of the approach it can be safely concluded that q is not constant for the purse-seine gear components of the 4WX fishery. As a result the abundance index from the purse-seine fleet has not been used to estimate input F in the SPA in recent years. An index of larval abundance has been more relied on.

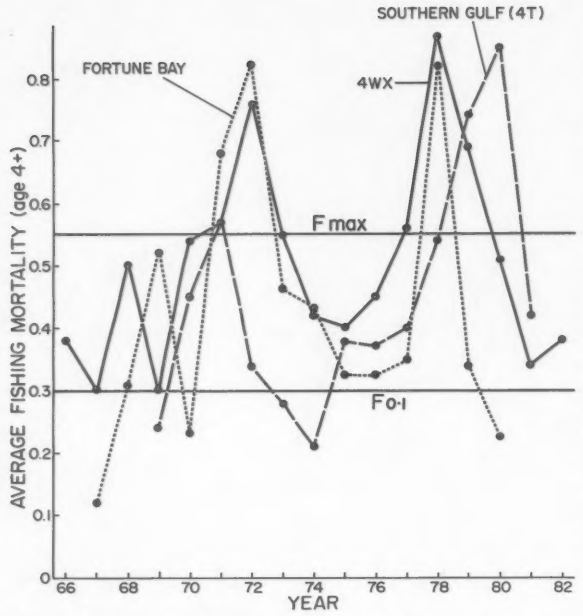

FIG. 3. Estimates of the trends in fishing mortality (average of age 4 and older ages) from recent stock assessments of the 4WX, southern Gulf of St. Lawrence, and Fortune Bay management units.

The third assumption identified is that the herring in the management unit have a stable age distribution. The sensitivity of this assumption in the use of the analytical yield model is evaluated for a range of species by Sinclair et al. (1983). It was shown that annual production of 4WX herring deviates markedly from maximum sustainable yields (MSY) as the age composition deviates in each direction from the stable age distribution. The reason for this is that when poor recruitment occurs several years in a row, for example, the production is concentrated in the older age classes which grow relatively more slowly. The yield-per-recruit model assumes that the biomass is distributed in a stable age distribution, with most of the production occurring in the younger age classes that grow relatively more rapidly. Under these skewed circumstances a recommended TAC is derived which can be considerably in excess of current population production. If the aim during low biomass periods is to protect a minimum spawning population size, a criterion such as the "$F_{0.1}$" is no longer appropriate. In the western Atlantic there has been no serious attempt to protect a minimum spawning stock biomass, as has been the case during recent years in the eastern Atlantic.

In summary, for the 4WX herring management unit it has been argued that the three assumptions identified in the assessment methodology are not adequately met. The consistent overestimates of abundance of herring shown in Fig. 2 and Table 4 were at least partially a result of the inapplicability of the second assumption (q is constant). The other two assumptions, we argue, can contribute to recruitment overfishing of individual spawning components within the management unit at relatively low F values for the unit as a whole.

General Discussion

From the above analysis of herring assessments in the western Atlantic some support can be given to the conclusions of the Aberdeen Symposium (Saville 1980b). An additional herring management unit (the southern Gulf of St. Lawrence, 3Pn and 4T) can be added to the long list of fishery collapses documented in that Symosium. Also, it has been confirmed that q increases as stock size decreases. This latter phenomenon has two effects. First, if the unadjusted catch rate index is used to fine tune SPA, biomass will be overestimated when stock size is decreasing. Second, the relative constancy of catch rates postpones economic overfishing, but at the expense of increased biological overfishing. The predictability in the temporal and spatial distributions of Atlantic herring, particularly those fished in tidally energetic seas, accentuates the catchability changes and contributes to overfishing. Atlantic herring in the Gulf of Maine area have been shown to be distributed seasonally in relation to tidally induced fronts which are found in the same geographic location from year to year (Sinclair and Iles 1985). Other species no doubt use oceanographic features in their migration, and as determinants of distribution patterns, but these features seem to be ephemeral, geographically speaking. The fish may "know" where the appropriate feature is, but since it is not easily identified it has little geographic predictability and the fishery has to search for the fish. In contrast, in the case of Atlantic herring in the Gulf of Maine area the fishermen can go out and wait confidently for the herring to arrive at the appropriate geographic location at a particular time. In other words, the species has a highly programmed life history with respect to time and space (Iles 1980). On August 1, give or take a few days, the prespawning aggregations form off southwest Nova Scotia, and the drift–gill net fishery begins. This predictability in time and space is not matched by most other commercially important species. These conclusions dealing with catchability changes and their causes are not original, but are worth repeating.

Two points, however, do merit identification here as additions to the conclusions of the Aberdeen Symposium: (1) the population structure of Atlantic herring is complicated in relation to management units; and (2) the stable age distribution assumption can lead to rapid decline in spawning biomass. It was concluded at the Aberdeen Symposium that all commercially exploited pelagic species are characterized by fishery collapses, with the exception of Atlantic menhaden (*Brevoortia tyrannus*) (Saville 1980b). It can be said that Pacific saury (*Cololabis saira*) is another notable exception (Matsumiya and Tanaka 1976). What is different between these two species and Atlantic herring, for example, that can account for their greater resilience? The crucial difference may well be the fundamental differences in their life history strategy, specifically their lack of stock richness. Both menhaden and saury spawn as single large populations with subsequent migrations (in the case of menhaden (Shaaf 1980), to diverse geographic locations). These two species are not broken up into many populations, and as such every fish in the management unit is in some sense equal (the sense in which "equal" is elaborated on below).

Atlantic and Pacific herring (and Atlantic mackerel (*Scomber scombrus*) to a lesser extent) are broken up into several spawning units with considerable between-population mixing at most phases of the life history. They are population rich. For example, if a Scots Bay herring (Sinclair and Iles 1985) can contribute progeny only to the Scots Bay population, which is on the order of 10 000 t, it is not "equal" in a management (conservation) sense to a northeast Georges Bank herring. The latter individual can contribute progeny to a population which

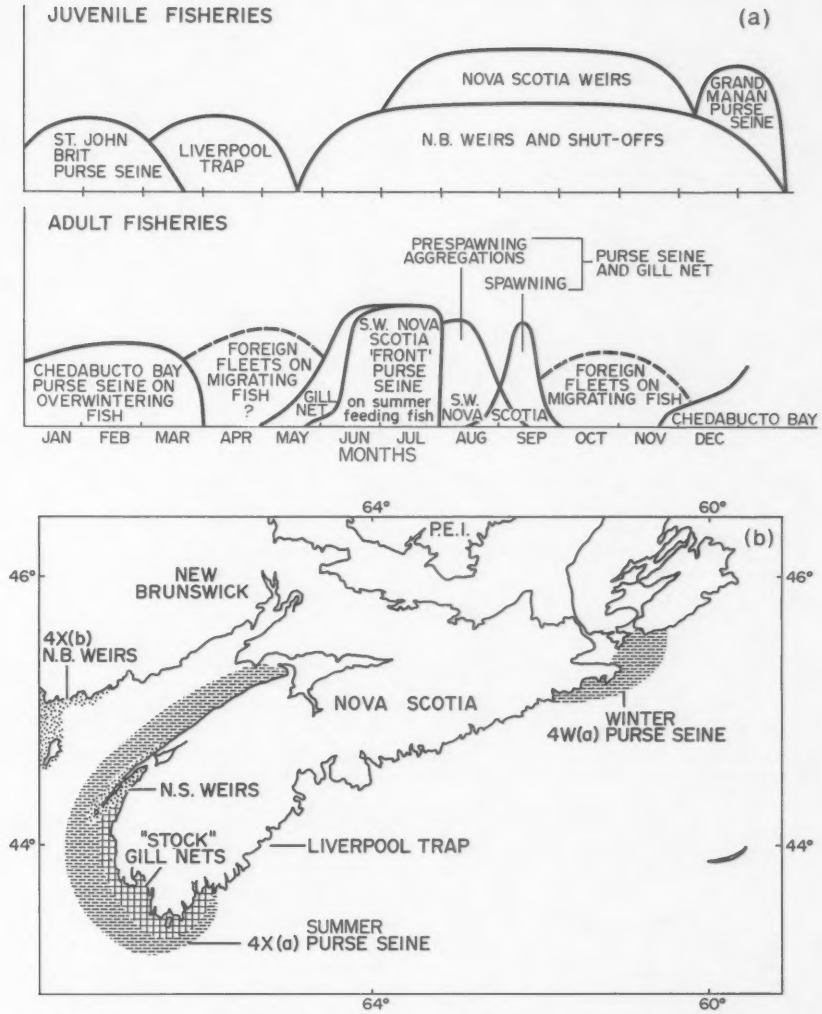

FIG. 4. (a) Seasonal components of the juvenile and adult fisheries in the 4WX management unit; (b) geographic location of the components of the herring fishery in the 4WX management unit. The different shadings indicate the various herring fisheries in 4WX.

can have a size of 1 million t (Anthony and Waring 1980); and yet both herring may be caught by a weir in the Bay of Fundy as juveniles within the same 4WX management unit. If one spawning population is lost by overfishing it cannot readily be repopulated by herring, even within the same management unit, which spawn in a separate location.

The difficulty of one spawning population repopulating another becomes clear if the stock hypothesis of Sinclair and Iles (1981b) and Iles and Sinclair (1982) is considered. In this hypothesis both the existence and the mean size of spawning populations are postulated to be a function of the existence of geographically fixed larval retention areas. The dual characteristics of homing to natal spawning areas (Sinclair and Iles 1985) and larval retention severely restrict the ability of one spawning population to repopulate contiguous overfished spawning areas. This difficulty, in the repopulation of an overfished spawning area, is well demonstrated by the lack of recovery to date of the northeast Georges Bank stock even though spawning has continued in the Nantucket Shoals area and off southwest Nova Scotia. On a longer time scale, however, repopulation and the establishment of new spawning populations must occur frequently. Many of the present spawning locations within the Gulf of Maine were above sea level several thousand years ago.

There is an important qualitative difference between herring and menhaden in this life history characteristic. Prudent management of a menhaden population should lead to rapid rebuilding to the carrying capacity and abundance levels observed prior to extensive fishing. In contrast, prudent management of Atlantic herring subsequent to the loss of several spawning populations within the management unit may lead in the short term only to rebuilding to the carrying capacity of the remaining spawning components. It is hypothesized here that it takes a relatively long time to reestablish "collapsed" herring spawning populations (e.g. Dogger Bank, Downs,

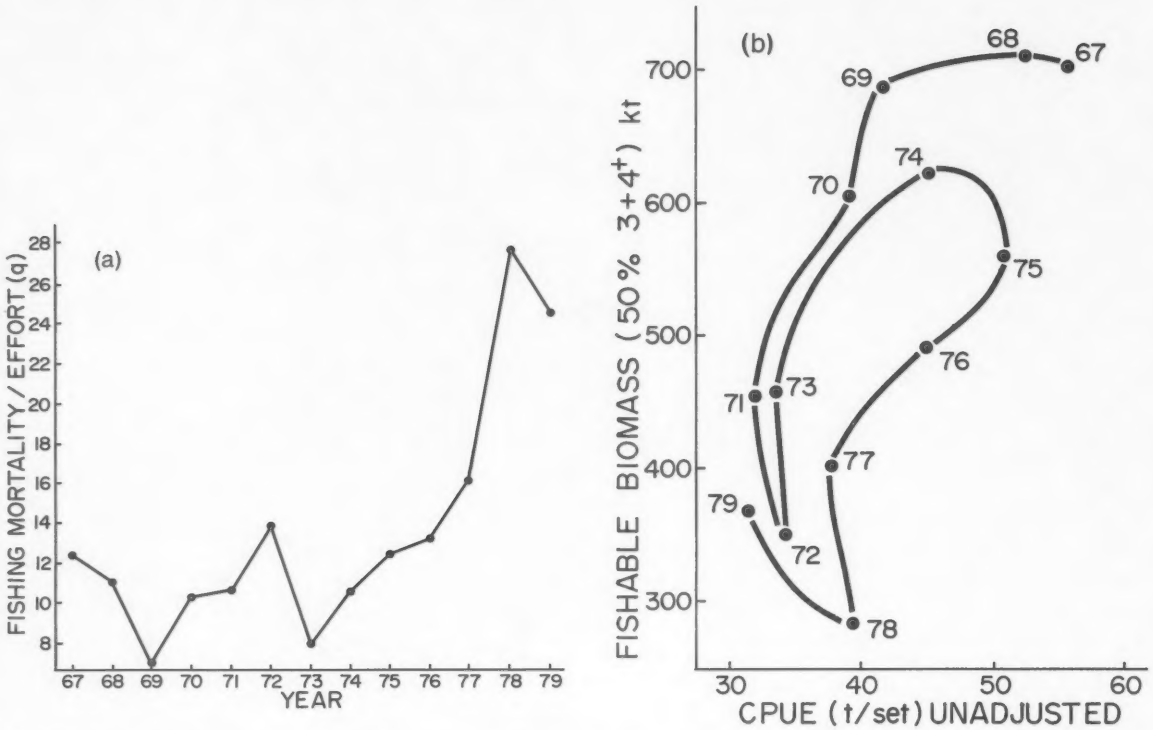

FIG. 5. (a) Catchability (q) changes for the "summer-feeding" purse-seine fishery off southwest Nova Scotia; (b) relationship between CPUE and population biomass from 1967 to 1979. (Both illustrations taken from Sinclair and Iles 1981a.)

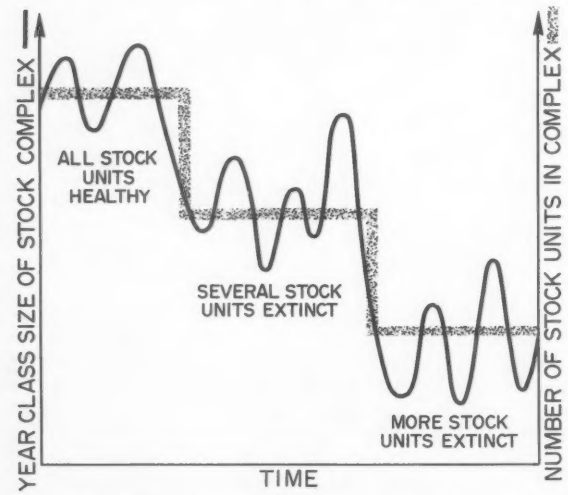
YEAR CLASS SIZE OF STOCK COMPLEX
NUMBER OF STOCK UNITS IN COMPLEX
ALL STOCK UNITS HEALTHY
SEVERAL STOCK UNITS EXTINCT
MORE STOCK UNITS EXTINCT
TIME

FIG. 6. Schematic representation of downward trend in recruitment to be expected as spawning components are overfished within a single management unit incorporating a stock complex (such as the southern Gulf of St. Lawrence or the North Sea).

Georges Bank) due to the particular life history features of herring, rather than due to environmental changes. The carrying capacity is argued to be defined at the larval stage (which is relatively discrete for the first several months and is supplied by homing of the spawning population to the specific geographic location characterizing the stock), rather than at the adult and juvenile mixed feeding phases.

A further complication is the difficulty in apportioning any desired level of fishing mortality homogeneously among the heterogenous component populations of any large management unit. If the fishery exploits the mixed phases of the distribution (juvenile phase, adult overwintering, and summer feeding), it is possible that some populations will experience a higher fishing mortality than others.

Perhaps more critical is that in a mixed stock management unit, for which a global quota is implemented, a very high fishing mortality can be applied to a given spawning component (either in the mixed phase or during the segregated prespawning and spawning phases) without the overall quota being exceeded and at moderate fishing mortalities for the stock complex as a whole. As a result, some individual populations can be lost from the management unit. One might expect to observe a cascading recruitment over time (Fig. 6), which is not susceptible to reversal in the short term, even with severe fishery restrictions (Georges Bank shows no sign of recovery after close to a decade without fishing). The Downs and Arcto–Norwegian stocks have recently shown signs of significant rebuilding after two or more decades following the respective collapses. Thus, the population structure in relation to the management unit is qualitatively different between some pelagics and the demersals. Due to this difference the susceptibility to recruitment overfishing is argued to be greater, and the time frame for recovery longer.

The second extension to the list of problems given at the Aberdeen Symposium results from the differential importance of the stable age distribution assumption in the analytical yield

model when pelagics and demersals are compared. Because of the lower recruitment variability in cod (*Gadus morhua*) and pollock (*Pollachius virens*), for example, and their relatively high growth rate at older ages, this assumption has been shown not to be as critical. For both Atlantic herring and Atlantic mackerel, however, it was considerably more important (Sinclair et al. 1983).

Conclusions

The verdict on the assessment of Atlantic herring in the northwest Atlantic is evident from Fig. 1 and 2. Stocks had declined greatly prior to the extension of jurisdiction over the continental shelf to the 200-mile limit, and population sizes have not been rebuilt subsequently. In fact, total catch continues to decline.

There are two categories of error. First is the consistent overestimation of population abundance in the analytical assessments. In many cases this has been due to the critical assumption that q is constant. Second, the management advice is argued here to be incapable of producing the predicted results, even if correctly applied. The assumptions in the assessment methodology (viz. (i) that the management unit is a population and (ii that it is distributed in the stable age distribution) generate fishing mortalities that can be too high (even though below F_{MSY} for most years), since they cannot be evenly distributed to ensure maintenance of the individual component spawning populations in the management unit.

If the above arguments are accepted, essentially that the management framework in place ($F_{0.1}$ derived quotas within the present management units) cannot adequately protect the existing Atlantic herring resource or lead to its rebuilding, what should be done? The management process should accept as a first guiding principle that all spawning populations within the management unit have to be sustained. It is not the overall F value for the management unit that is critical, but rather the criterion that the maintenance of each spawning component within the unit is essential for sustained recruitment. This could involve a move away from managing according to a specific overall annual exploitation level to an emphasis on distributing an arbitrarily low level of exploitation (say $F = 0.2$) more evenly through seasons and geographic locations. Qualitative criteria (i.e. less effort seasonally distributed) should override quantitative methodology (i.e. $F_{0.1}$ derived annual TAC's for management units based on statistical reporting areas). Atlantic herring should be managed in the conceptual framework of a salmon biologist (i.e. to ensure optimal return to each spawning river) rather than as viewed by a groundfish biologist. This could entail a significant reduction of fishing effort on the mixed phases of the life history (e.g. the adult summer-feeding and overwintering fisheries). It is inferred here that the mixed stock fisheries, in which it is not possible to partition fishing mortality amongst the contributing stocks, have contributed to the overexploitation of herring stocks. This inference cannot be demonstrated, but is a reasonable interpretation of past events. In this respect it should be noted that a high and continuous catch was recorded for over a century by the spawning fisheries in both the Gulf of St. Lawrence (Tibbo et al. 1969) and the North Sea (Holden 1978). In these examples the unstated management philosophy, restricting the fishing mortality to the spawning population themselves, resulted in effective stock protection and high biological yield. The relative constancy in catch generated the conditions for a stable Atlantic herring industry.

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Estuarine Growth of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) as Inferred from Otolith Microstructure

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Neilson, J. D., G. H. Geen, and D. Bottom. 1985. Estuarine growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. Can. J. Fish. Aquat. Sci. 42: 899–908.

The growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the Sixes River Estuary, Oregon, was inferred from otolith microstructure. Otolith increments appeared to be formed daily, on average, and a transition between those produced during freshwater residence and estuary residence was apparent. Otolith microstructure was also examined with respect to time series of water temperature, population density, and benthic standing crop data. While the results supported the hypothesis of food-limited growth, elevated water temperatures in midsummer may have decreased food conversion efficiencies, thus also contributing to an observed growth rate decline. It was also found that from counts of otolith increments formed during freshwater life, fish that hatched relatively late tended to spend less time in freshwater before moving downstream to the estuary.

La croissance du saumon quinnat (*Oncorhynchus tshawytscha*) peuplant l'estuaire de la rivière Sixes (Oregon) a été déduite de la microstructure des otolithes. Les zones de croissance semblent se former quotidiennement, en moyenne, et une zone de transition entre celles qui sont déposées en eau douce et celles qui sont déposées en eau estuarienne était apparente. La microstructure des otolithes a aussi été examinée en fonction de séries chronologiques de données sur la température de l'eau, la densité des populations et la biomasse benthique. Quoique les résultats étayent l'hypothèse d'une croissance limitée par la présence de nourriture, les températures élevées de l'eau au milieu de l'été peuvent avoir diminué l'efficacité de conversion des aliments, contribuant ainsi à la baisse observée du taux de croissance. Le dénombrement des zones de croissance déposées sur les otolithes pendant le séjour en eau douce a aussi révélé que les poissons nés relativement tard ont tendance à passer moins de temps en eau douce avant la dévalaison vers l'estuaire.

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Juveniles of three Pacific salmon species (chinook, *Oncorhynchus tshawytscha*; coho, *O. kisutch*; and chum, *O. keta*) may reside in estuaries for significant periods prior to ocean migration. Estuaries provide opportunities for seawater acclimation and feeding prior to entry into the sea. Chinook salmon juveniles, although not obligate estuary dwellers, utilize estuaries to the greatest extent (Dorcey et al. 1978; Healey 1982) and often spend several months in the estuary before migrating to the ocean. Levy and Northcote (1981) suggested that the duration and quality of estuarine residence might be a determinant of subsequent marine survival of chinook salmon. The size attained by juvenile Pacific salmon prior to entering the sea is considered critical by many workers, so rapid growth during the period of estuarine residence may confer advantages. Larger salmon smolts adapt better to higher salinities (Hoar 1976) and may be less vulnerable to predation (Parker 1971). Schlucter and Lichatowich (1977) found that the size attained by juvenile chinook salmon after estuarine residence and by the end of their first year influenced subsequent growth and age at maturity. Simenstad et al. (1982) suggested that salmonids use estuaries as refugia from predators, and as physiological transition areas for optimum availability of preferred food organisms which promote rapid growth. Those authors noted, however, that the quantitative significance of such factors to the ultimate survival of adults is not well established.

One of the few who attempted to quantify the significance of estuarine residence was Reimers (1973). He found that of the five juvenile life history types thought to exist among Sixes River chinook salmon, those that spent 3–4 mo in the estuary following a freshwater residence of similar duration comprised over 90% of returning adults. That percentage was considerably greater than that expected based on the relative proportions of different life history types that occurred in juveniles, possibly indicating a greater rate of survival to maturation.

Reimers (1973) also suggested that in years of high population abundance, a reduction of juvenile chinook salmon growth rate occurred while fish were in the estuary. He hypothesized a density-dependent growth reduction related to prey availability.

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To test Reimers' hypothesis, Oregon Department of Fish and Wildlife (ODFW) staff have collected several years of data on the abundance of Sixes River juvenile chinook salmon. In 1980, prey availability, quantity of prey consumed, and estuarine water temperature data were also obtained. The substantial data record on Sixes River chinook salmon populations also provides an opportunity to assess other factors that might affect estuarine growth of chinook salmon.

In this paper, we describe the use of otolith microstructure to assess the relative significance of environmental variables such as water temperature, population density, and prey abundance. In addition, examination of otolith microstructure within the population permitted an assessment of the variability in the time at which estuarine residence commences, and estuarine growth in relation to previous freshwater life history, including duration of freshwater residence, freshwater growth rate, and size at entry to the estuarine environment.

Although scale circuli were used by Reimers (1973) to assess patterns of estuarine residence and growth, otolith microstructure offers greater resolution and precision due to the greater frequency with which regular structural features are formed (Pannella 1971). In addition, regression models of fish size on otolith size often give better fits than do models of fish length and scale radii for salmonid data (Jonsson and Stenseth 1977). This paper represents one of the first applications of otolith microstructure to interpretation of field data which go beyond a more detailed description of age and/or growth. Moreover, confidence in the interpretation of otolith microstructure is increased, as data in our previous papers (Neilson and Geen 1982, 1984a) have provided a better appreciation of the effect of various photoperiod, feeding, and temperature regimes on otolith increment production.

Methods

Description of the Study Area

The estuary of the Sixes River (Fig. 1) is located 80 km south of Coos Bay, Oregon, and 110 km north of the Oregon–California border (42°58′N, 124°33′W). The river drains 340 km^2 of the coastal and Klamath mountains, dropping approximately 290 m to sea level over a distance of 56 km (Bottom et al. 1983). Mean daily discharge ranges from 0.5 m^3/s in the summer to more than 200 m^3/s in the winter (Reimers 1973).

Tidewater extends about 4 km upstream from the mouth of Sixes River. However, most of the research has been confined to the broad, shallow embayment in the lower 1 km of the river (Fig. 1). Sediments in this area are primarily gravel, or sand and gravel. Maximum depth at high tide is approximately 5 m, although most of the lower estuary is only 1–2 m deep during seasonal low flows.

Reduced outflows and strong northwest winds cause a shallow sand sill to build at the mouth of the Sixes River during the summer. When the sill is fully developed, seawater enters through a narrow gap in the sill only near high tide; there is a net outflow from the estuary 75% of the time. Throughout most of the summer the estuary is stratified during the period of outflow with as much as 10–25‰ salinity difference between surface and bottom layers of the shallow bay (Reimers 1973). During the flood tides, water mixes rapidly near the mouth and saltwater moves slowly upstream along the bottom.

Two species of tube-dwelling amphipod, *Corophium salmonis* and *C. spinicorne*, and the gammarid amphipod *Eogammarus confervicolus* represent 71–92% of the total number and 62–78% of the total biomass of prey consumed by juvenile chinook salmon in the Sixes River estuary through 1978–80 (Bottom et al. 1983). The standing crop of *Corophium* usually peaks in late June and declines in abundance through the summer.

Sixes River chinook salmon are a "fall" race, with the adults entering freshwater in the fall of each year and spawning from December to March. After about 3 mo, fry and a smaller number of yearlings move down into the estuary beginning in May or June and are the most abundant salmonids in the Sixes River estuary through the summer. Population estimates of juvenile chinook salmon over the past 15 yr have ranged from 59 000 to 269 000 during the midsummer period. Young-of-the-year reside in the estuary until October or November, ranging in size from approximately 40 mm in the spring to 110–130 mm in mid-October. Size at migration to the sea from the estuary varies with population abundance and the productivity of the Sixes River estuary in a particular year (Reimers 1973).

In general, the Sixes River estuary is typical of the small estuaries associated with watersheds draining the Klamath Mountain region of Oregon. It is not directly comparable with larger, more northern estuaries supporting chinook salmon populations such as the Fraser River in British Columbia.

Field Sampling

Juvenile chinook salmon were sampled by ODFW personnel in the Sixes River estuary (Fig. 1) in 1979, 1980, and 1981. Samples of fish used for otolith microstructure examination (n = 15) were collected from seine hauls at approximately biweekly intervals from May through September. The daily ration was determined in 1980 only. Water temperature was recorded continuously in 1980 by thermographs located at the surface and bottom of the estuary near where fish were captured.

Population size was estimated four times in 1980 using the Bailey-modified Peterson single census mark–recapture procedure (Ricker 1975), and catch-per-unit-effort (CPUE) statistics. The census was conducted throughout the estuary. Fish were collected with seines over a 2- to 3-d period and marked with a brand cooled with liquid nitrogen. The use of different brands for successive population estimates allowed ODFW personnel to estimate the population abundance at each period. However, no correction for loss of tagged fish through mortality or emigration was made, a procedure that may significantly inflate the population estimate.

Inferences regarding prey availability were made on the basis of benthic standing crop data and stomach content weights. Daily rations were also calculated using Elliott and Persson's (1978) methods.

Preparation of Otoliths and Data Analyses

Otoliths from juvenile chinook salmon were prepared for microstructure examination following the methods outlined by Neilson and Geen (1981). Where otolith increment widths are reported, the data were derived by digitizing increment widths along a standard radius on enlarged scanning electron microscope photographs (Neilson and Geen 1982). Preparations were coded and examined in a random sequence to avoid bias in the interpretation of otolith microstructure.

Back-calculations of lengths at age were made from otoliths

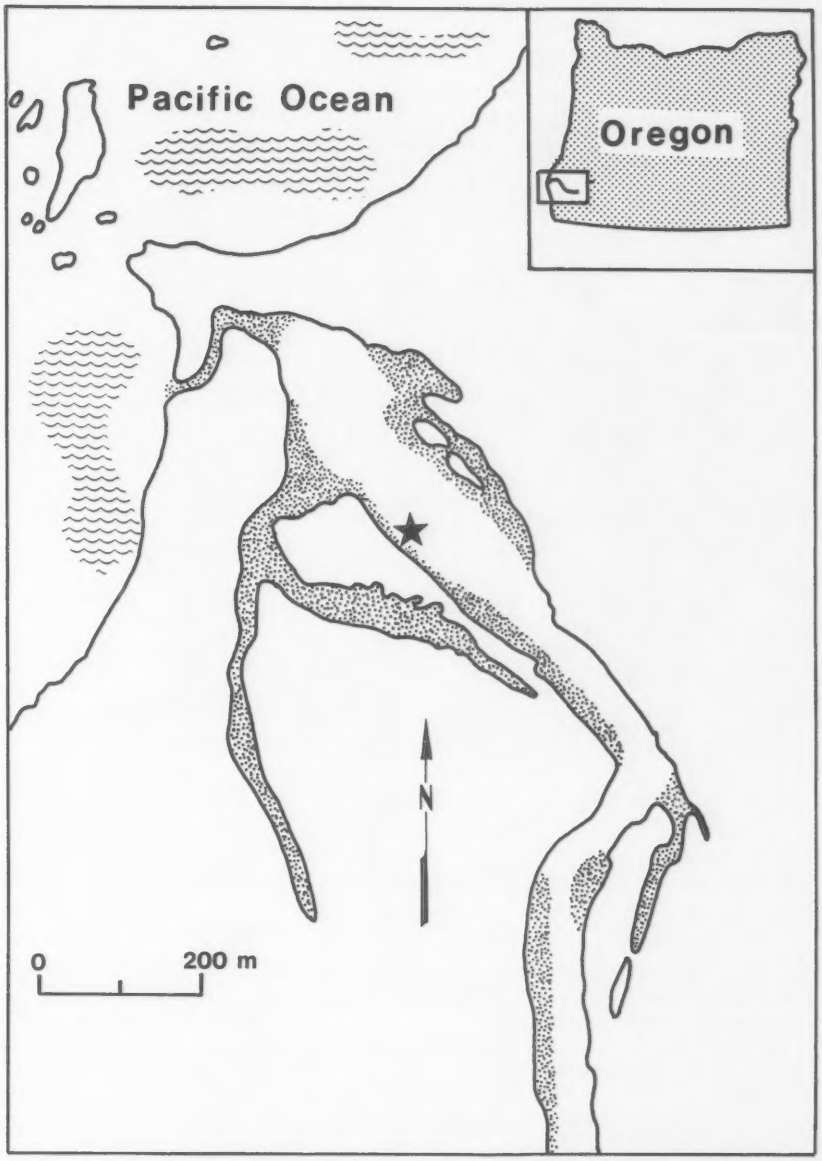

FIG. 1. Sixes River estuary showing the sampling location (★) in 1980.

of juvenile chinook salmon using Lee's method as described by Carlander (1981). Length at age is given by the following equation:

$$\hat{L}_i = a + \frac{L_c - a}{S_c} S_i$$

where S_c = the otolith length at capture, S_i = the otolith length at age i, L_c = the length of the fish at capture, $\hat{L}_i$ = the length of the fish at age i, and a = the y-intercept of the fish length – otolith length regression.

In developing the fish length – otolith length relationship, we used otolith length as the independent variable rather than otolith radius. The presence of multiple otolith precursors, or primordia, in chinook salmon (Neilson and Geen 1984b) created difficulty in locating the centre of the otolith for radius measurements. We used geometric mean regressions for the fish size – otolith size relationships, as natural variability was associated with both axes (Ricker 1973). Measurements of otolith length were made from images projected on a microfiche viewer. We made two independent sets of measurements on the coded series of preparations. In cases where measurements differed by >10%, the preparation was excluded from further examination. Using this criterion, we rejected 14% of the preparations. A total of 255 left-side sagittal otoliths were

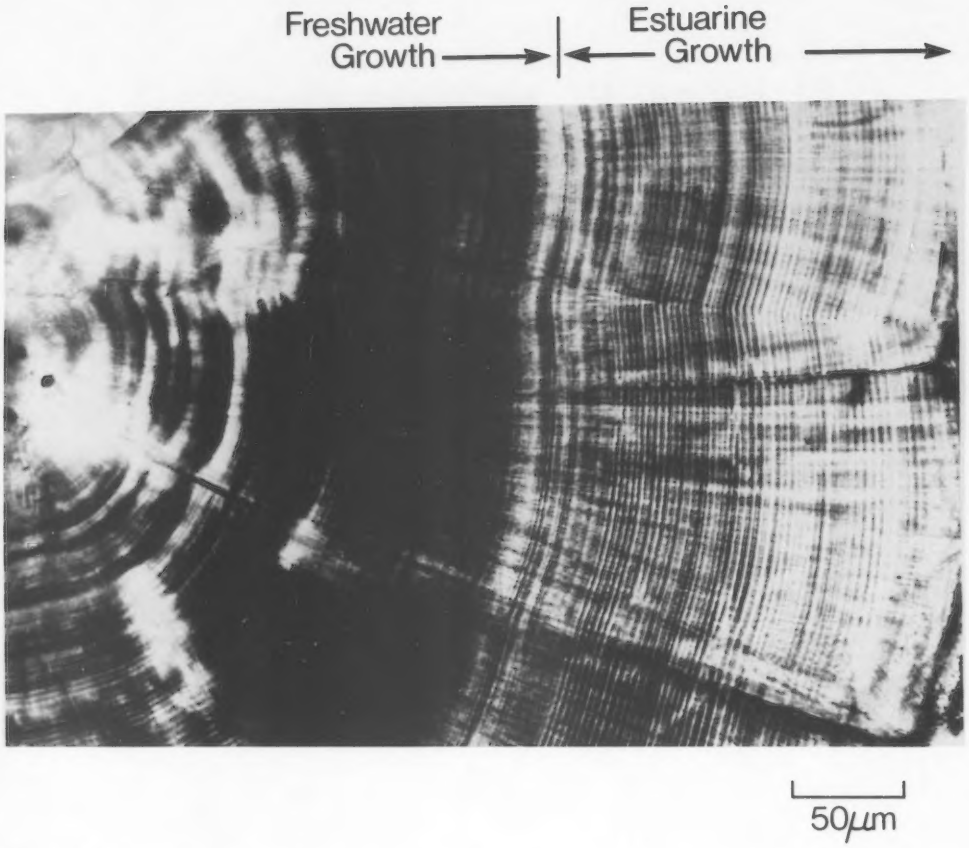

FIG. 2. Polished section of a juvenile chinook salmon sagittal otolith showing microstructure differences associated with movement from freshwater to the estuary.

examined with the microfiche viewer during the study. Of that total, 60 were randomly selected and examined with a scanning electron microscope for determination of increment widths.

Results

To study estuarine growth using otolith microstructure, we first described the relationship between fish size and otolith size and determined the frequency of otolith growth increment formation. The relationships between fish length (x) and left otolith total length (y) are adequately represented by the following geometric mean linear regressions (r^2 and significance calculated using the arithmetic mean regressions):

Year of sample	n	Geometric mean regression equation	Coefficient of determination (r^2)	Significance
1979	87	$y = 0.021(x) + 0.515$	0.77	0.0001
1980	69	$y = 0.033(x) - 0.280$	0.78	0.0001
1981	99	$y = 0.032(x) - 0.125$	0.81	0.0001

Analysis of covariance (using arithmetic mean regressions) and the Student–Newman–Keuls test indicated that the slope of the regression of otolith length – fish length data in 1979 samples was significantly less ($p < 0.0001$) than the slopes of the 1980 and 1981 regressions. For that reason, separate regressions for each brood-year were retained for back-calculations of fish length at age.

The rate of growth of juvenile chinook salmon downstream migrants increased markedly upon entry into the estuarine environment, reflected in greater otolith increment widths (Fig. 2). The criterion for determining the beginning of estuarine residence was that point at which increment width increased 25% or more relative to the mean of the previous 10 increments, and was sustained over at least 20 consecutive increments or to the otolith periphery. Increments formed in freshwater averaged <3 μm in width, whereas the estuarine growth increments formed in early summer were >4 μm. The close correspondence between increased increment width and the migration from freshwater to the estuary is supported by data from the biweekly fish collections from the Sixes River estuary. In 1981, the first migrants in the estuary were taken on May 4, and had 0–14 ($\bar{x} = 4.5$) estuarine growth increments. Examination of otoliths from fish caught above the estuary also provided a means of characterizing known freshwater growth increments and verified our ability to differentiate between increments formed in freshwater and in the estuary.

Estuarine growth increments appeared to be formed daily. We determined the frequency of formation by comparing the mean observed increase in estuarine increment counts versus the expected increase in increment counts assuming a daily frequency of formation in consecutive biweekly samples. To calculate the expected number of growth increments, we took the Julian day of first capture each year and subtracted 14 d to account for the interval between biweekly samples. That date was assumed to be the first day of estuarine residence. Because of how we calculated the date of commencement of the estuarine rearing period, increment counts were generally less than expected, although not significantly so. The slope of arithmetic mean regressions of observed increment counts on expected increment counts did not significantly differ from unity for the 1979, 1980, or 1981 data (t-tests, $0.05 < p < 0.10$), indicating that one otolith growth increment was formed every 24 h, on average (Fig. 3).

As we did not have sequential samples of chinook salmon from freshwater, evidence that otolith increments were formed once every 24 h in freshwater is indirect. Averages of 72.4 ± 15.9, 86.6 ± 20.3, and 72.4 ± 19.3 freshwater growth increments were counted in otoliths from juvenile chinook salmon samples from 1979, 1980, and 1981, respectively (±1 SD indicated). The counts were reasonably consistent with the number of days elapsed from peak emergence to peak numbers of fish migrating downstream into the estuary (approximately 75 d) plus approximately 10 d as otolith increment production begins before hatching and emergence (Neilson and Geen 1984b).

Estuarine Growth in Relation to Freshwater Growth and Residence

The calculated mean size of chinook salmon migrants entering the estuary did not differ significantly between years (Fig. 4, analysis of variance, $p = 0.0538$), nor did the average date of estuarine entry vary significantly as indicated through otolith microstructure examination (Fig. 5, analysis of variance, $p = 0.1007$). Regressions of back-calculated size at estuarine entry on date of estuarine entry (Julian day) were not significant ($p = 0.1129$, 0.7129, and 0.2615, respectively). Regressions of freshwater age (number of increments) on date of estuarine entry (Julian day) were significant in 1979 and 1981 ($p = 0.0044$ and 0.0030, respectively) and not significant in 1980 ($p = 0.1836$). Regression equations for the 1979 and 1981 data are as follows:

$$(1979) \quad y = -1.30(x) + 267.1$$

$$(1981) \quad y = -0.68(x) + 170.3$$

where y is number of increments formed in freshwater and x is Julian day. The negative slopes of the geometric mean regressions indicate that as summer progressed in 1979 and 1981, migrants entering the estuary were younger on average.

To assess whether late migrants into the estuary showed different trends in growth than did earlier migrants, we randomly selected 10 fish that arrived in the estuary before May 24, 1981 (the mean date of estuarine entry), and compared the pattern of estuarine growth as indicated by otolith microstructure with that of 10 fish that had entered the estuary after May 24. The mean date of entry into the estuary was May 17 and June 25 for the samples of "early" and "late" migrants, respectively. After the deposition of a series of relatively wide increments assumed to correspond with the beginning of estuarine residence, increment widths gradually declined. Neither the peak increment width (t-test, $0.05 < p < 0.10$) nor the rate of increment width decline differed significantly (analysis of covariance, $0.10 < p < 0.20$), indicating that no differential growth was associated with different times of entry into the estuary.

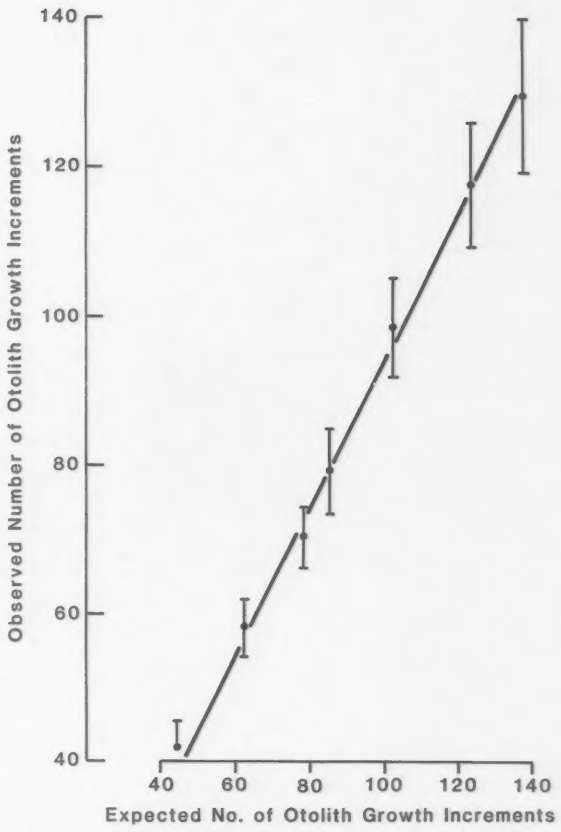

FIG. 3. Arithmetic mean regression of counts (±1 SE) of estuary growth increments versus expected number of increments for otoliths of Sixes River juvenile chinook salmon, 1981.

Estuarine Growth in Relation to Environmental Factors

The average growth rates of fish, expressed as mean otolith increment width, increased markedly in May and June during the period corresponding to estuarine entry (Fig. 6). Thereafter a gradual reduction in increment width was observed in all 3 yr, an indication of declining growth rate. The reduction in otolith increment width was more noticeable in 1980 than in 1979, as analysis of covariance for data from June 1 to September 24 indicated that the slope of the regression of mean increment width on time was significantly greater in 1980 than in 1979 (analysis of covariance, $p = 0.0020$). The reduction in increment width in 1980 reflected a slower growth rate. The reduced slope of the otolith length – fish length relationship in 1979 compared with 1980 further contributed to the growth rate difference, as a given increase in otolith length corresponded to a greater increase in fish length. Increment width maxima coincided approximately with the beginning of reduced fish growth. The instantaneous daily growth rate in June 1980 averaged approximately 5% based on change in fork length,

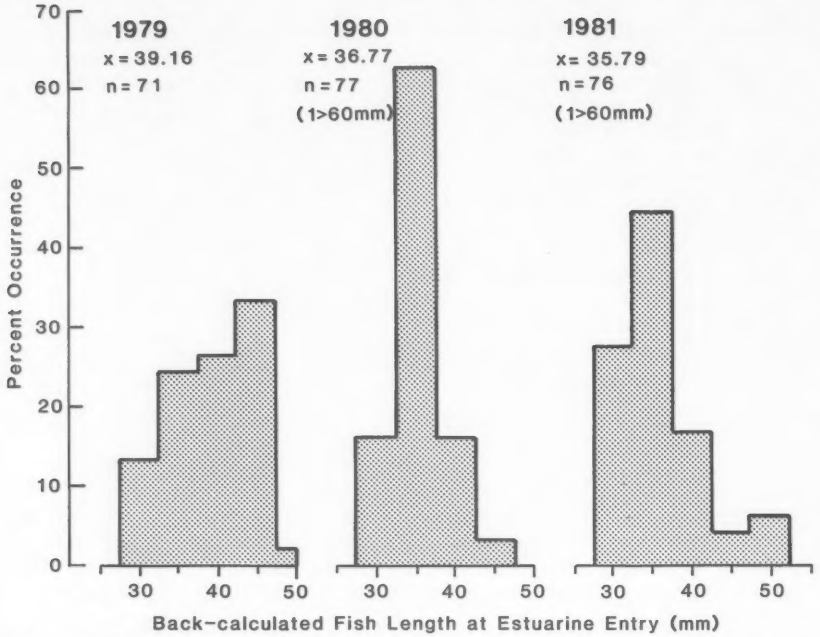

FIG. 4. Size distributions of juvenile chinook salmon entering the Sixes River estuary in 1979, 1980, and 1981 determined by back-calculation from otolith microstructure and size at capture.

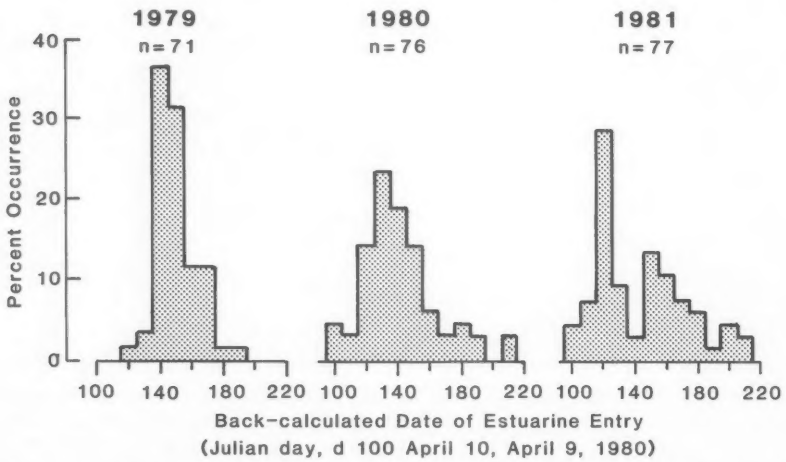

FIG. 5. Date of entry of chinook salmon migrants into the Sixes River estuary in 1979, 1980, and 1981 as determined from otolith microstructure.

corresponding to increment widths of about 3.5 μm (Fig. 6). By late August, the instantaneous daily growth rate was 2% or less, corresponding to increment widths of about 2 μm. While data shown were for fish caught at the end of the estuary rearing period, similar patterns of otolith microstructure were found in earlier captures with relatively large increment widths corresponding with entry into the estuary and decreasing widths as the summer progressed.

We attempted to relate the observed pattern of otolith growth to environmental conditions in the estuary in 1980, the year for which most complete data were available. Peak numbers of benthic amphipods occurred after the average growth rate of chinook salmon (expressed by mean increment width) had started to decline (Fig. 7). Other indicators of prey availability, including wet weight of stomach contents and daily rations, did not decrease until after the average growth rate had declined.

Discussion

To address the apparent anomaly shown in Fig. 7 of decreased growth rate despite continued high levels of benthic standing crop, we examined the water temperature record

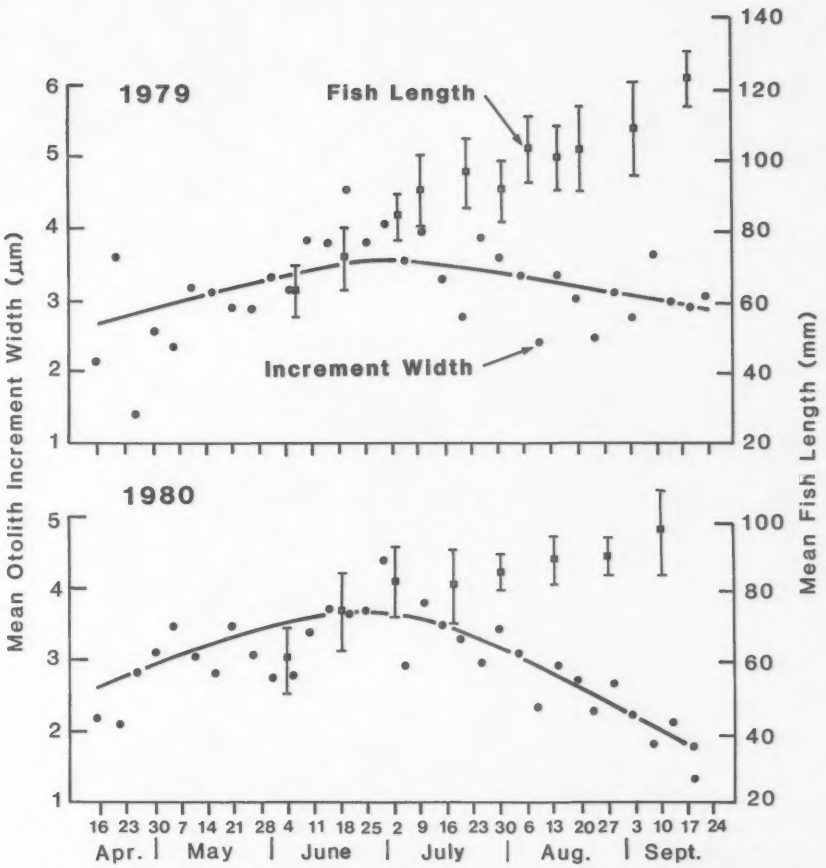
1979
Fish Length
Increment Width
1980
Mean Otolith Increment Width (μm)
Mean Fish Length (mm)
16 23 30 7 14 21 28 4 11 18 25 2 9 16 23 30 6 13 20 27 3 10 17 24
Apr. | May | June | July | Aug. | Sept.

FIG. 6. Mean increment width (●) versus time as determined from otoliths of juvenile chinook salmon caught in the Sixes River estuary, late September, 1979 and 1980 ($n = 10$ for each year). Curves are fitted using the method of cubic splines with delta (a root-mean-square weighting factor) equal to 0.5. Average size (±1 SE) of juvenile chinook salmon caught in biweekly seine hauls is also indicated (■).

during the rearing period (Fig. 8). While water temperatures ranged between approximately 12 and 15°C prior to July 1 (during the period of rapid growth), they were generally higher later in the summer and frequently exceeded 18°C. The latter interval coincided with the period of reduced growth (Fig. 6). Brett et al. (1982) inferred a temperature – growth rate relationship for chinook salmon fry based on fish fed to satiation and his previous studies with sockeye salmon, concluding that for fish fed 0.6 of the satiation ration, optimum growth occurred at 14.8°C. Warmer temperatures resulted in lower conversion efficiencies and decreased growth. In our study, it seems likely that fish were receiving rations less than the satiation level, as the average stomach content weight was 1–2% of wet body weight (Bottom et al. 1983) compared with other published data such as Healey's (1980) Nanaimo River study where fish consumed up to 5% of wet body weight. Thus it seems possible that the inferred relationships of Brett et al. (1982) account for the phenomenon of decreased growth rate observed here.

Other features of the estuarine environment in 1980 may have contributed to the decreased growth rate. The relatively low stomach content weight may reflect intraspecific competition for the scarce food resource. The maximum potential for such competition occurs in July when the estuary population peaked (Fig. 9) coincident with the onset of warmer water temperatures. Bottom et al. (1983) provided further data supporting the notion of food-limited growth in 1980, noting that the mean biomass and number of *Corophium* sp. in chinook salmon stomachs were generally lower in early and midsummer 1980 compared with 1979, when the midsummer growth rate depression was less pronounced (Fig. 6).

Density-dependent growth in Sixes River juvenile chinook salmon has been suggested in past studies (Reimers 1973; Bottom et al. 1983). However, previous workers hypothesizing density-dependent growth rate reductions in the Sixes River were not able to dismiss the possibility that observed mean growth rate reductions were artifacts resulting from the inclusion of recently recruited smaller fish in the samples. In our study, examination of otolith microstructure has provided growth records for individual fish whose date of entry to the estuary is known and has provided support for Reimers' (1973) hypothesis that density-dependent growth rate reductions occur during the residence of chinook salmon in the Sixes River estuary.

Healey (1982) has reviewed evidence for growth reductions

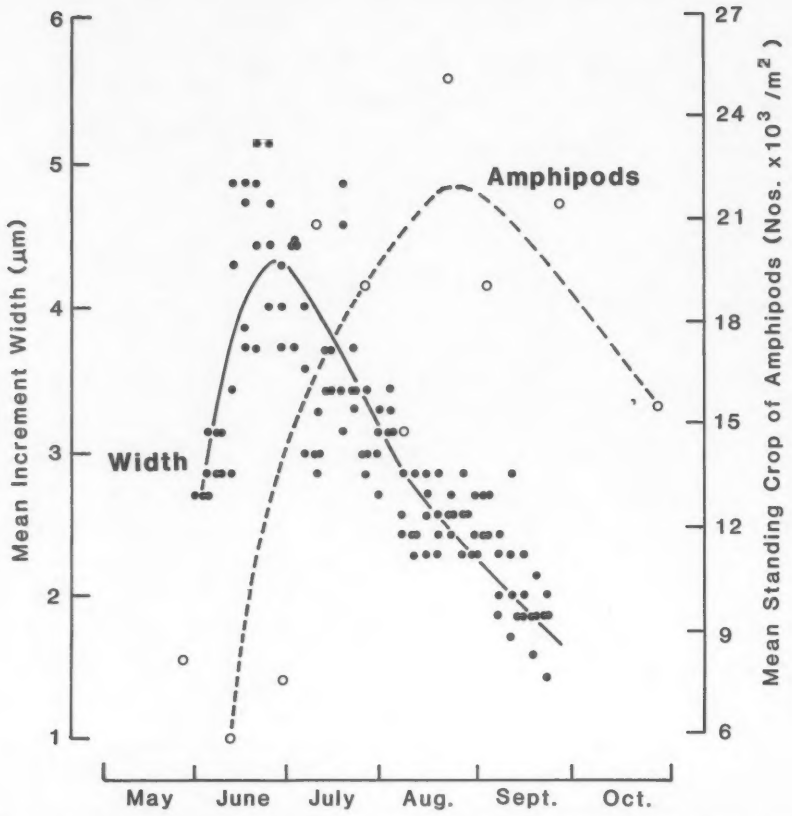

FIG. 7. Mean benthic standing crop (five replicates) of *Corophium spinicorne*, *C. salmonis*, and *Eogammarus confervicolus*, the three major prey species of juvenile chinook salmon in the Sixes River in 1980. The relationship of mean increment widths versus time is also shown. The curves were fitted by eye.

of Pacific salmon in more northern estuaries. The only other systems where growth reductions were thought to occur were the estuaries of the Squamish River, B.C., and the Yaquina River, Oregon. However, given the apparent variability of growth rate of juvenile chinook salmon in the Sixes River from year to year, density-dependent growth rate reductions in juvenile salmon rearing in other systems not closely studied on an annual basis may be a more common occurrence than is currently thought.

The back-calculated sizes of fish on entry into the estuary underestimated their true size somewhat. This was particularly apparent in 1981, when the mean back-calculated fork length was 35.8 mm. Among fish caught on May 4, 1981, those that by our criterion of otolith microstructure had entered the estuary that day averaged 40.0 mm fork length (range 38–41 mm, n = 5). The bias could have been caused by an inappropriate back-calculation procedure or by a misinterpretation of the beginning of estuarine residence from examination of otolith microstructure. However, the Lee method of back-calculation employed here is widely used and generally considered appropriate (Carlander 1981). The linear otolith length – fork length relationships also seemed adequate, as examination of residual plots of the unexplained variance gave no indication of curvilinearity. The possibility of misinterpretation of the beginning of the estuarine residence period is not readily dismissed, as no independent confirmation methods were available such as tetracycline marking (Campana and Neilson 1982; Neilson and Geen 1984a). However, as the bias towards underestimating the true size seems systematic, our conclusions are robust for comparative purposes. Other authors who have noted systematic errors in back-calculated lengths from otolith measurements include Hickling (1933), Halliday (1969), and Reay (1972).

In the absence of artificially induced time markers there was some uncertainty regarding the frequency of increment formation. While our comparison of observed versus expected increment counts indicated that one increment was formed every 24 h, the technique was not precise due to the long period over which fish are recruited to the estuary population. However, the increment widths were consistent with those formed in our laboratory experiments. E. B. Brothers (3 Sunset West, Ithaca, NY, pers. comm.) and English (1981) also found that juvenile chinook salmon form one increment every 24 h in marine environments. In the field, the frequency of increment formation could be determined by examining otoliths of chinook salmon held in pens located in the estuary. However, even if increments are not formed once every 24 h, it is still likely that increment widths are proportional to fish growth and have utility for growth studies, if the frequency of increment formation is assumed constant.

The marked visual contrast which aided identification of

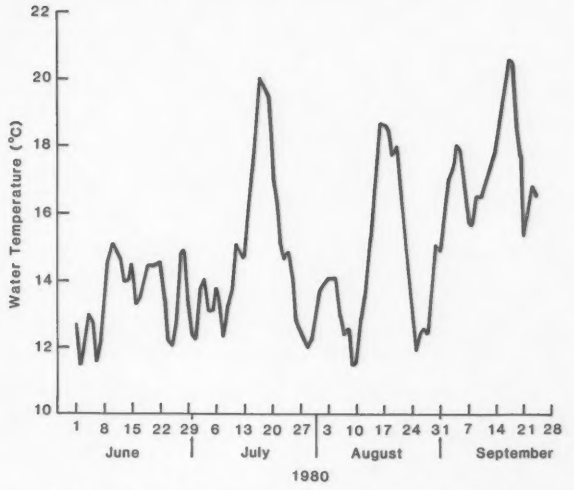

FIG. 8. Mean daily water temperature (measured by a thermograph located near the estuary bottom) in the Sixes River estuary, 1980.

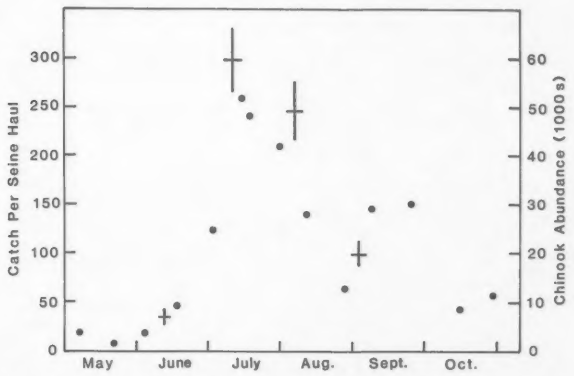

FIG. 9. Chinook salmon population abundance in the Sixes River estuary in 1980, estimated from Bailey-modified mark–recapture and catch-per-unit-effort statistics (●). The upper and lower confidence intervals of the mark–recapture estimates are also shown.

estuarine growth increments may have reflected the greater amplitude of water temperature fluctuations in the Sixes River estuary relative to temperature fluctuations in the river. We have shown that diel temperature fluctuations of 2–4°C amplitude resulted in increased visual contrast of growth increments, compared with otoliths from fish reared in a constant-temperature regime (Neilson and Geen 1984a). In the Sixes River, diel temperature fluctuations, while present, were irregular in occurrence and amplitude compared with the estuary. River temperatures ranged through 3.5 ± 1.5°C (mean daily) amplitude measured ~20 km upstream of the estuary (±1 SD indicated), in May 1979, the only year in which temperature data were available for early summer. During a corresponding period in 1980, mean daily fluctuations in the estuary were 5.9 ± 1.0°C. Fish might also be exposed to daily temperature fluctuations if they exhibited a diel vertical migration through the thermally stratified water column (up to 10°C) of the estuary. Volk et al. (1984) have also noted a transition in otolith microstructure as juvenile chum salmon leave freshwater, as has M. Bradford, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. (pers. comm.), in a preliminary study of otolith microstructure of Yakoun River pink salmon (*O. gorbuscha*).

A concern regarding the application of otolith microstructure examination to wild populations is the apparently large number of environmental stimuli which affect increment number and width under laboratory conditions (Neilson and Geen 1982, 1984a). In nature, it seems likely that many cyclic phenomena of various periods exist which could cause deviation from the one increment every 24 h relationship. Sixes River juvenile chinook salmon, however, did not show significant deviations from the one increment per 24 h rate of increment production. Twice daily temperature cycles, as might be expected under tidal influence, did not occur in the estuary although there were marked diel fluctuations. Similarly, while some diel periodicity in gut contents was noted, it was weak and irregular in occurrence. The absence of regularity in feeding or temperature fluctuations may have precluded formation of more than one growth increment every 24 h as could be produced in laboratory experiments.

It may be that while there is a variety of possible cyclic cues in the environment, they may be functional only if the cycle has certain characteristics. From an energetic perspective, it may be advantageous for fish to be in phase with the most constant cue to concentrate feeding behavior, for example, at critical times of the day. If circadian rhythms serve primarily to concentrate appropriate behavior at certain times of the day, cyclic cues not in phase with the optimum activity periods might not influence fish. Such a phenomenon is known as frequency demultiplication (Marler and Hamilton 1967) and might explain why apparently only one increment was formed every 24 h in the otoliths of Sixes River chinook salmon, despite the possibility of cues with a period less than 24 h.

We examined the effects of different freshwater life history patterns on timing of estuarine entry and subsequent growth and found a negative correlation between date of estuarine entry and freshwater age in 2 of 3 yr studied. The earlier emigration of fish developing from eggs deposited relatively late in the spawning season may have been due to increased river temperatures, a mechanism suggested by Reimers (1973). Alternatively, part of the life history strategy associated with progeny of late spawners may include an abbreviated period in freshwater with the result that fish benefit from better growth while in the estuary. However, our examination of otolith microstructure indicated that while otolith increment widths in fish arriving in the estuary relatively late in 1980 increased upon estuarine entry, the rate of growth inferred from increment widths did not differ significantly from that of early recruits to the estuary population. It may be that late migrants leave the estuary at a smaller average size than earlier recruits to the estuary, assuming no differential duration of residence in the estuary.

Many workers have commented upon the importance of estuaries as rearing habitat for Pacific salmon juveniles. However, prior to the use of otolith microstructure examination as a tool for detailed study of age and growth, it has been difficult to quantify fish growth in estuaries relative to other habitats without extensive mark–recapture programs. This paper has identified the relationships between fish growth rate, expressed through otolith mean increment width and environmental conditions in the estuary. We present evidence that growth of juvenile chinook salmon in the Sixes River estuary is density dependent and limited by food availability. Among possible alternative hypotheses that might explain the apparent decline in

growth rate, two of the most likely are size-selective mortality or emigration. While we have unpublished data that do not support the occurrence of size-selective mortality of fish during estuary residence, we cannot discount the possibility that size-selective emigration exists.

It is difficult to comment on the applicability of our results to other stocks, as the feeding options available to Sixes River chinook salmon differ significantly from those in other estuaries. As noted by Bottom et al. (1983), the food web of the Sixes River estuary is simple and consists of relatively few fish or invertebrate species. Sixes River chinook salmon do not feed on the infaunal taxa found throughout the estuary, but consume only the large epibenthic crustaceans. In contrast, chinook salmon in larger Oregon estuaries consume a greater variety of prey, including insects and larval fish (Forsberg et al. 1977; Myers 1980). Among British Columbia estuaries, chinook diets are variable, but adult insect and decapod larvae are frequently important (Sibert and Kask 1978; Levy and Northcote 1981; Healey 1982).

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An Evaluation by Field Experiments of the McLay Model of Stream Drift

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The model of McLay (J. Fish. Res. Board Can. 27: 359–370) for describing the drift of stream organisms was tested in a variety of field experiments in which organisms were disturbed from the substrate and/or the natural drift was blocked. In each situation, appropriate corrections may be made for the catch of drift organisms by the sampling nets. Disturbed animals drifted at a rate much less than stream velocity. The logarithm of the distance travelled was a linear function of the logarithm of mean stream velocity and conformed to the McLay model. Similarly, the model adequately described experiments in which two disturbances were done simultaneously, when drift was blocked for a 2-h period, and when there was both disturbance and blockage. A more comprehensive version of the model was only partially successful in describing the drift at various distances downstream of a blockage sustained for 4 d, probably because of upstream migration of organisms through the substrate, spatial differences in the densities of animals in the substrate, or a reduction in drift rate at lower density in the substrate.

Le modèle élaboré par McLay (J. Fish. Res. Board Can. 27 : 359–370) pour décrire la dérive des organismes lotiques a été vérifié dans une série d'expérience sur le terrain au cours desquelles les sédiments ont été remués pour en extraire les organismes et la dérive naturelle, a été entravée. Dans chaque situation, on peut apporter des corrections appropriées pour la capture d'organismes dérivants dans les filets d'échantillonnage. Les animaux dérangé ont dérivé à un taux très inférieur à la vitesse du courant. Le logarithme de la distance parcourue était une fonction linéaire du logarithme de la vitesse moyenne du courant et était en conformité avec le modèle de McLay. De même, le modèle décrivait adéquatement les expériences où deux perturbations étaient faites simultanément, où la dérive était bloquée pendant 2 h et où des perturbations et des blocages avaient lieu. Une version plus complète du modèle n'était que partiellement efficace pour la description de la dérive à diverses distances en aval d'une obstruction maintenue pendant 4 jours, probablement à cause de la migration intra-substrat des organismes vers l'amont, de différences spatiales entre les densités des organismes présents dans le substrat ou de la baisse du taux de dérive à des densités inférieures dans le substrat.

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The model of McLay (1970) for describing the drift stream organisms has a number of implications which enable a test of its validity by various types of field experiments. The stream bed may be disturbed one or more times in one or more places to create pulses of drift for which the rate of settling may be inferred from what remains in the drift. Alternatively, the natural drift may be removed (blocked), the pattern of drift downstream reflecting the blockage in a predictable way. This paper describes the theoretical considerations and a series of experiments which were used to test the theory.

Theoretical Considerations

McLay (1970) presented a simple model for describing downstream drift of stream organisms. A pulse of organisms introduced into the stream flow by a disturbance returns to the substrate according to the simple negative exponential relationship:

$$(1) \quad N_X = N_0 e^{-RX}$$

where N_0 is the number of organisms introduced by a disturbance, N_X is the number of organisms in the stream at distance X from the point of introduction, and R is a constant reflecting the rate of settling to the substrate, and may be descriptive of a single species of organism or an aggregate of species.

For this formulation, the mean distance travelled by a drifting organism ($\bar{X}$) is

$$(2) \quad \bar{X} = \frac{1}{R}.$$

This model was tested, particularly with respect to the effect of stream velocity, by Elliott (1971a) who suggested that the rate of settling (R) could be related to modal stream velocity (V)

by

$$(3) \quad R = aV^{-b}$$

where a (Elliott's A^{-1}) and b (Elliott's B) are constants, typical of particular species.

Substituting the mean velocity for the modal velocity, which is reasonable in situations of relatively uniform gradient and stream cross section, equations (2) and (3) are readily combined into a single expression of mean distance travelled ($\bar{X}$):

$$(4) \quad \bar{X} = \frac{V^b}{a}.$$

If the natural drift process is viewed as the consequence of a spontaneous emergence which is the equivalent of a disturbance along the whole stream length, the amount of natural drift (N_{max}) is given by the integral of an equation such as equation (1) for values of X from zero to infinity, i.e.

$$(5) \quad N_{max} = \frac{N_s}{R}$$

where N_s is the number of organisms that emerge spontaneously per unit distance.

Downstream from a blockage, such as a screen removing all of the drifting organisms, the number in the drift at a given distance downstream (N_X) is given by

$$(6) \quad N_X = N_{max}(1 - e^{-RX}).$$

Note that if there is a disturbance of the stream bed, a pulse of organisms is added to the natural drift, and the total number in the drift is

$$N_X = N_0 e^{-RX} + N_{max}.$$

In field experiments, N_{max} is measured by nets placed above a disturbance and may be subtracted from the observed drift to obtain that related to the disturbance.

If there is a blockage of the stream and a disturbance of the stream bed immediately below the blockage, then

$$(7) \quad N_X = N_{max}(1 - e^{-RX}) + N_0 e^{-RX}$$

and if the width of stream bottom disturbed is chosen such as to make N_0 equal to N_{max}, then the number in the drift at all distances downstream is constant and equal to N_{max}.

For the natural drift process described above, the unit of time is best considered as a whole day, or more properly a night, it being typical of most stream organisms to drift mainly by night. To assume that there is more than a single detachment per night is unnecessarily inconvenient. (The same organism drifting twice may as well be considered as two organisms.)

Additionally, note that in the natural system the number of animals that settle must equal the number that spontaneously emerge, for what comes down, must have gone up.

When sampling is conducted at several points (i) at equal intervals of distances downstream from a disturbance, and the sampling takes a significant proportion of the drift, allowance must be made for the removal of drifting organisms by samples taken upstream from any particular point. Thus, the sample estimate of N_X for a net at distance j downstream from the source, when another sampling net is upstream at distance i from the source, assuming complete mixing, is

$$(8) \quad N_{X_j} = (1 - c)N_0 e^{-RX_j}$$

where c is the proportion of the drift organisms captured by the sampling at point i and which is assumed constant for all nets at all distances.

Similar but more complex equations can be constructed on the same principle for nets that are downstream from several sampling nets.

If there is more than one disturbance, the number in the drift at a distance downstream will be the sum of those expected from each of the two disturbances plus those that would have been in the drift from each disturbance if they had not been caught by sampling upstream.

A parallel line of argument applies to sampling of natural drift. Thus, if the natural stream drift is blocked and there is a sampling station upstream, the sample estimate of N_{X_j} is

$$(9) \quad N_{X_j} = N_{max}[(1 - c)(e^{-RX_{j-i}} - e^{-RX_j})].$$

For all of the foregoing there are standard procedures for nonlinear least squares minimization which enable estimation of values of N_{max}, c, and R, given values of N_{X_j}.

If a blockage of a stream is sustained for several days and nights it would be expected that there would be a progressive impoverishment of substrate organisms, for those that drifted downstream would not be replaced from upstream. In these circumstances, the consequences of the model formulation are more complex. At each distance downstream from the blockage there is a recruitment to the substrate from all distances upstream. This recruitment diminishes as the upstream areas become progressively more impoverished. To construct an analytical model it is convenient to represent the process as being continuous, i.e.

$$(10) \quad \frac{\delta N_B}{\delta t} = -\lambda N_B + \mu N_D$$

$$(11) \quad \frac{\delta N_D}{\delta t} + \frac{v \delta N_D}{\delta x} = \lambda N_B - \mu N_D$$

where N_B is the population density in the stream bed, N_D is the population density in the drift, λ is the instantaneous probability of an organism entering the drift, μ is the instantaneous probability of an organism settling from the drift, v is the stream "velocity" as measured by the rate at which the organisms are displaced per unit time, and x is the distance from the blockage.

Equation (10) depicts the process of departure and entry of organisms at each point of the stream bed, while equation (11) depicts the augmentation of the drift at any point by that which is coming from upstream, both of which in total must equal that which arises into the drift less that which settles. Note that λ is the equivalent of m and N_B is the equivalent of k/m of the colonization model of Sheldon (1977).

The general solution to these equations (available from the senior author on request) is expressed in terms of Bessell functions, but it may be computed for sufficiently small values of x and t from the series:

$$(12) \quad \frac{N_B}{N_{B_0}} = 1 - e^{-(X+T)} \sum_{n=0}^{\infty} \frac{T^n}{n!} 1 + X + \frac{X^2}{2!} + \ldots \frac{X^{(n-1)}}{(n-1)!}$$

$$(13) \quad \frac{N_D}{N_{max}} = 1 - e^{-(X+T)} \sum_{n=0}^{\infty} \frac{T^n}{n!} 1 + X + \frac{X^2}{2!} + \ldots + \frac{X^{(n-1)}}{(n-1)!} + \frac{X^n}{n!}$$

where N_{B_0} is the initial (natural) population density of organisms in the stream bed and N_{max} is the natural population density of

organisms in the drift and where

$$X = \frac{\mu x}{v}$$

and

$$T = \lambda\left(t - \frac{x}{v}\right).$$

A typical solution to these equations demonstrates the progressive impoverishment of the stream bed below a continuous blockage (Fig. 1). For any series of drift sample data the model is to be fitted so as to minimize the sum of squares of deviation of N_D/N_{max} by an appropriate choice of λ and μ.

In all of the foregoing, the units of measurement of N_X and N_{max} are not numbers of organisms per specified area or per unit stream width. In field experiments, both quantities are most conveniently expressed as number of organisms per sampling net per unit time, which will have local implications about the total abundance of organisms in the drift and in the stream bottom.

General Methods

Field experiments were conducted to test the McLay model in artificial spawning channels at Jones Creek near Hope (49°19′N, 121°37′W) and at Gates Creek near Pemberton (50°32′N, 122°33′W), both in British Columbia. These channels are of uniform width (Jones Creek 4.25 m; Gates Creek 6.09 m), with a uniform gravel composition (Jones Creek 0.64–3.18 cm, depth 40 cm; Gates Creek 1.27–10.16 cm, depth 40.6 cm). In Jones Creek there are wooden baffles at intervals of 30 m to control depth and velocity.

The technique of disturbance was simply kicking up the substrate by shuffling across the stream, a method that Morgan and Egglishaw (1965) suggested is most effective and that McLay (1970) used when his model was developed. The strip of stream disturbed from bank to bank was 22 cm wide. Blocking of stream drift was accomplished with a series of 30 × 30 cm filtering nets mounted on a wood baffle in Jones Creek and placed on the bottom in Gates Creek. In all experiments, sampling downstream of the disturbance or the blockage was done with nets 10 cm wide × 30 cm high. Water depths were always less than 30 cm. Both kinds of nets were made of 471 μm nitrex, shaped in a right cone to a length of 45 cm for the sampling nets and 95 cm for the larger filtering nets. At the distal end of each net a bottomless 9-cm-diameter plastic bottle was attached (the top of the bottle could thus be taken off and the contents removed without moving the net). The nets were mounted on 0.95-cm round stock steel frames on which washers were welded so that the nets could be slipped over steel stakes driven into the stream substrate. The stakes were invariably placed in the stream at least 24 h before an experiment began.

The positioning of sampling nets was similar throughout all of the experiments. Three control nets were placed 2 m upstream of the disturbance or blockage to measure natural drift levels. Downstream, nets were placed at various measured distances from the disturbance or blockage at sites chosen at random across the width of the stream with the restriction that no net was directly downstream from any other.

Stream velocity was recorded at each net opening and numbers of organisms collected were corrected for differences in volume of water filtered by dividing the average velocity by the net velocity (depth was also recorded but was uniform so the correction is essentially for volume filtered).

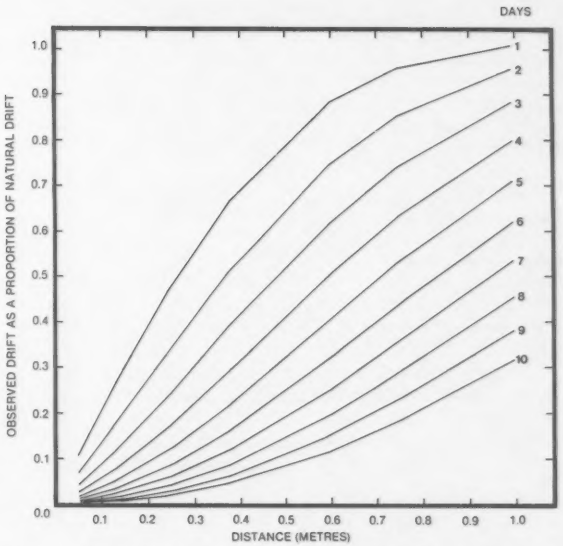

FIG. 1. Prediction from a mathematical model of the drift as a proportion of natural drift on successive days below a site of continuous complete blockage.

The analysis of the data was in most cases by an iterative process, using a nonlinear function optimization routine (SIMPLEX) which fitted the unconstrained function by least squares, and which took into account the removals by sampling nets upstream (equations (8) and (9)). In some of the simpler experiments in which only such equations as (1) and (6) were the model, a log transform was considered appropriate if the variance was correlated with the mean.

Results

Repeated Disturbance of the Same Area of Substrate

A preliminary series of trials was undertaken at Jones Creek to estimate the proportion of the organisms in the substrate that were disturbed. In each of four daytime trials, a 22-cm-wide strip was disturbed six times at 2-min intervals, and after the last disturbance the gravel was removed and examined for evidence that some organisms have not been disturbed. Sampling of the disturbed animals was by 30 × 30 cm nets immediately downstream of the area of disturbed substrate. Data was fitted by regression of log number caught against number of disturbances.

The percentage of organisms leaving the substrate from the first disturbance (of the total that were caught from six disturbances) varied from trial to trial (Table 1) but was close to 50% for the organisms that were sufficiently abundant for good estimates. Hence, the method used was consistent in removing, in the first disturbance, a relatively constant percentage of those common animals that were "disturbable."

The less abundant species showed a greater apparent variation which would be expected because of the small sample size. Nevertheless, the range of the average number of three mayfly species (*Ephemerella*, *Cinygmula*, and *Paraleptophlebia*) coincided with that of the more common species (i.e. between 40 and 60% of the total displaced were caught at the first

TABLE 1. Percentage of the total number of disturbed organisms displaced from the stream gravel bed by the first of a series of six disturbances (*samples contained less than 10 organisms).

Organism	Trial 1	Trial 2	Trial 3	Trial 4	Mean
Total	51	42	51	51	49
Baetis sp.	51	48	57	48	51
Epeorus sp.	51	45	48	52	49
Ephemerella sp.	50*	67*	—	—	—
Cinygmula sp.	38*	—	—	44*	—
Paraleptophlebia sp.	67*	63*	59	—	—
Simulium sp.	25*	—	—	—	—
Others	61	54	63	59	59

TABLE 2. Average percentage of organisms that left the substrate in each of six successive disturbances of the substrate in each of four trials.

Trial	Total	*Epeorus*	*Baetis*	Remainder
1	42	42	39	39
2	57	50	75	73
3	55	51	74	65
4	44	47	45	34
Mean	49.5	47.5	58.3	52.8

disturbance). *Simulium* sp. was not easily disturbed into the drift though it was very abundant on the disturbed rocks.

Regressions of log number of organisms against number of disturbances for the total, for the most abundant organisms *Epeorus* and *Baetis*, and for the remainder listed in Table 2 were all significant. There was no heterogeneity of slopes amongst trials except for *Baetis*. The percentages of animals disturbed (antilogs of slopes) were in the range from 34 to 75% with means for each group centred around 50%. The method is evidently fairly consistent and each disturbance removes roughly 50% of the remaining "disturbable" organisms.

Rate of Downstream Displacement of Organisms

The rate at which invertebrates drift may not be the same as the stream velocity, and the rate at which drift moves is relevant to the length of time nets are maintained if they are to catch the organisms displaced by a disturbance. A preliminary experiment was conducted at Jones Creek.

Three 10 × 30 cm nets were placed at 22:00 at each of four stations at distances of 1, 2, 3, and 5 m below a disturbance, and three immediately above the disturbance to measure natural drift. Each set of three nets was placed at locations chosen at random within the right, left, and central thirds of the stream width. Two of the three nets chosen at random were sampled at each time; samples were taken at 7.5, 15, 30, 60, and 120 min after a disturbance.

After correcting for velocity, the number of organisms captured was divided by the time the net had been sampling and expressed as a catch rate.

The average stream velocity was 47.3 cm/s, so the organisms would pass the 5 m station in approximately 11 s if drift was moving at the stream velocity. In the first 7.5 min the drift from the disturbance was roughly 10 times the natural drift at all stations, and in the second 7.5 min roughly 5 times. Thereafter, the catch at all stations was less than the natural drift (Table 3).

TABLE 3. Average catching rate (per 7.5 min) of drift organisms in nets placed at various distances downstream of a disturbance.

Sample time (min)	Natural	Distance from disturbance (m) 1	2	3	5
0–7.5	34	399	285	194	311
7.5–15	32	118	158	108	83
15–30	35	10	13	15	23
30–60	43	18	19	27	30
60–120	27	18	21	18	10

Evidently, the disturbed organisms had settled within 15 min, but the average rate of drift is much less than the stream velocity. The same trend was not observed for the dominant organisms, *Epeorus* sp. and *Baetis* sp.

It seems likely that disturbed organisms enter the drift, return to the substrate, and subsequently reenter the drift, and this accounts for a rate of displacement slower than stream velocity. The lower than natural levels of drift after 15 min are curious and are seemingly too consistent to be accounted for by natural variation in drift. Two contributing factors could be (1) the lack of a contribution to the drift from the disturbed area subsequent to the disturbance and (2) possible effects of the disturbance on the organisms in the stream bed immediately downstream.

Distance Travelled by Disturbed Organisms

If the McLay model is appropriate the number of disturbed organisms in the drift declines exponentially with distance. In each of two trials at Jones Creek and in eight trials at Gates Creek, a 22-cm-wide strip across the channel was disturbed. Three sampling nets were placed in the stream at each of the distances 1, 2, 3, 5, 10, and 20 m downstream of the disturbance and three nets measured natural drift upstream. Nets were raised at either 0.5 or 1 h after the disturbance, the time varying from trial to trial. All trials were between 22:00 and 24:00. Velocity was varied in the Gates Creek trials by setting the headgate valves of the channel at 08:00, 14 h before the trial. All catches were corrected for velocity at the net opening, and all data analysis took account of the catch by sampling nets upstream of other sampling nets (in the fashion described by equations (8) and (9)).

The pattern of catches (Fig. 2) indicated a fair agreement to the form of the McLay model although in some instances there was considerable disparity in the natural drift observed in the control nets and that estimated from the nonlinear fitting routine (Table 4). A similar adequate fit (not shown) was apparent for the most abundant organisms *Epeorus* sp. and *Baetis* sp., but for other groups, which were much less abundant, the fit was satisfactory but influenced by the small sample sizes.

From equation (4) the relationship between log velocity and log mean distance travelled should be linear, which is reflected in Fig. 3 for the Gates Creek trials for the total of all organisms, *Epeorus* sp., and *Baetis* sp. for which the correlation coefficients were respectively 0.84, 0.70, and 0.98.

For the less abundant species, most travelled further at higher velocities. There were some that did the reverse but the sample sizes were too small to be conclusive (*Cinygmula* sp. and *Paraleptophlebia* sp. were examples).

Additivity of Drift from Two Disturbances

Four trials were conducted at Jones Creek, for which the

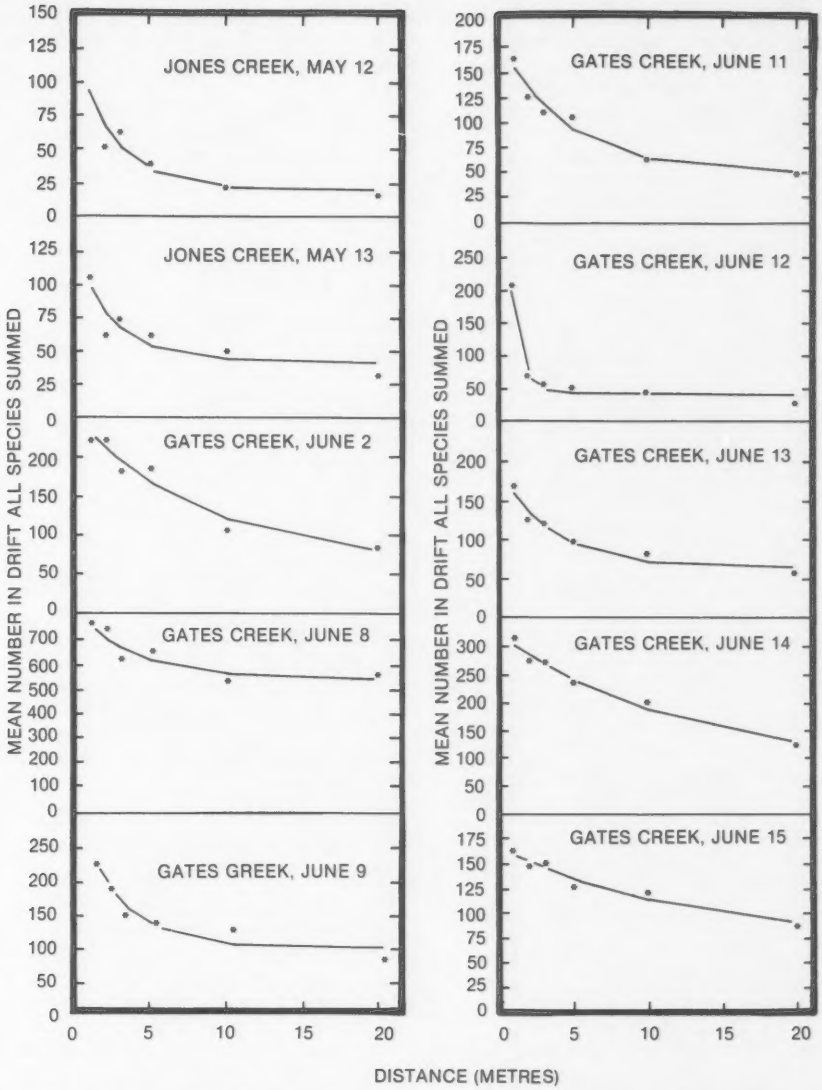
JONES CREEK, MAY 12
JONES CREEK, MAY 13
GATES CREEK, JUNE 2
GATES CREEK, JUNE 8
GATES GREEK, JUNE 9
GATES CREEK, JUNE 11
GATES CREEK, JUNE 12
GATES CREEK, JUNE 13
GATES CREEK, JUNE 14
GATES CREEK, JUNE 15
MEAN NUMBER IN DRIFT ALL SPECIES SUMMED
DISTANCE (METRES)

FIG. 2. Line of best fit, for all species summed, of mean number of drift organisms caught at various distances downstream from a disturbance of the stream bottom.

design and procedure were similar to those for single disturbance experiments. On the first two trials, the disturbances were 5 m apart and sampling nets were set at 1, 2, 4, 6, 7, 8, 10, 15, and 20 m below the upstream disturbance. In the second two trials, the disturbances were 10 m apart and nets were placed at 1, 4, 9, 11, 12, 13, 15, 20, and 30 m. In each trial, three control nets were placed 2 m above the first disturbance. The nets remained lowered for 0.5 h, some time between 22:00 and 24:00.

The nonlinear routine gave a good fit to model values (using a variant of equation (8)) to observed values (Fig. 4). The differences between observed and estimated natural drift for the summed species were small (Table 5). Similar results were apparent for the most abundant groups of organisms.

There were significant differences in the numbers disturbed at each of the two sites, varying from 27 times as many at the first site to 5 times more at the second site. On one occasion, the estimated contribution from two sites was within three animals of being equal. Evidently there are substantial differences in density of organisms in the substrate in different areas.

In each of the separate trials the numbers of organisms in individual taxa and for all taxa summed conformed to the predicted relationship, although the number contributed by each of the disturbances was not the same.

Blockage of Drift

A series of interlocking nets (30 × 30 cm) was placed across the spawning channel to filter all of the stream flow and thus prevent downstream movement of drift organisms. Down-

TABLE 4. Observed natural drift and estimates of natural drift, number disturbed, rate of return, and mean distance travelled for 10 disturbance experiments, the first 2 of which were in Jones Creek in May 1971 and the remainder in Gates Creek between June 1 and 15, 1973. All trials were conducted between 22:00 and 24:00.

Trial	Observed natural drift (control nets)	Estimated natural drift, N_{max}	Estimated number disturbed, N_0	Rate of return to substrate (R)	Mean distance travelled (m), X	Velocity (m/s), V
1	19	19	109	0.417	2.40	0.766
2	28	41	84	0.429	2.33	0.58
3	96	63	183	0.120	8.36	0.456
4	475	548	272	0.302	3.31	0.473
5	101	101	168	0.361	2.77	0.370
6	80	49	132	0.211	4.73	0.330
7	53	44	894	1.719	0.58	0.260
8	95	64	129	0.277	3.62	0.340
9	114	69	254	0.072	13.85	0.490
10	67	67	102	0.074	13.57	0.650

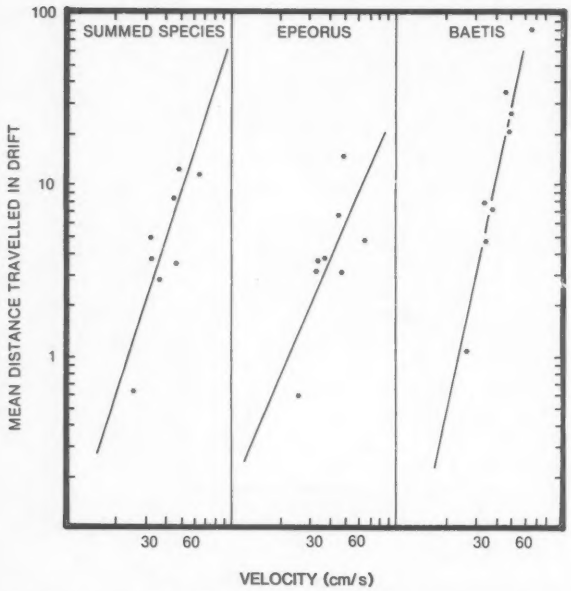

FIG. 3. Log–log regression for Gates Creek of the average distance travelled by drift organisms against stream velocity for summed species ($Y = 0.07 + 3.05x$), *Epeorus* ($Y = 0.15 + 2.25x$), and *Baetis* ($Y = 0.01 + 4.58x$).

stream of the blockage, groups of three sampling nets were placed at distances of 1, 2, 3, 5, 10, and 20 m, one net in each of three sections of stream width. Three control nets were placed 2 m upstream of the blockage nets. Two trials at Jones Creek and one at Gates Creek were conducted between 22:00 and 24:00 h and one trial in daytime at a light intensity of 21 100 lx at Jones Creek.

In all trials there was a good fit to the McLay model (equation (8)), as evidenced by the close approximation of the line of best fit to the data (Fig. 5). Differences in the amount of drift and the rate of return in the various trials (Table 6) reflected differences in velocity and the different species mix in the two localities and by day and night. The dominant genera at Jones Creek were *Cinygmula*, *Parameletus*, *Paraleptophlebia*, *Epeorus*, and *Lepidostoma* but at Gates Creek, *Epeorus* and *Baetis* dominated. At Jones Creek, *Lepidostoma* comprised 75% of the drift by day but only 13% by night.

The difference between the observed drift above the blockage and the estimated natural maximum drift downstream was small in three of the trials, but large in one of the night trials in Jones Creek. There were also a few instances of major discrepancies of this kind for individual genera. Presumably these differences reflect differences in abundance of organisms in various parts of the stream bed.

Disturbance and Blockage of Drift

A series of interlocking 30 × 30 cm nets was placed across Gates Creek spawning channel completely filtering all organisms drifting downstream. Immediately below this blockage, a strip of stream bed, in one case 11 cm wide and in the other 22 cm wide and extending from one side of the stream to the other, was disturbed. Sampling nets in groups of three were placed at distances of 1, 2, 3, 5, 10, and 20 m downstream.

In theory, if the width of the disturbed strip is appropriate then the amount of drift should be constant at all distances downstream, and this appeared to be roughly the case when the width of the strip was 11 cm (Fig. 6). Note that because this technique of disturbance puts roughly 50% of the stream bed organisms into the drift, N_{max} equals one half of the benthic animals in an 11-cm strip of stream bed. With a greater width (22 cm) the slope of the regression of number of organisms against distance was more negative than at 11 cm, conforming to theoretical expectations. It is to be noted that the theoretical expectation is not a straight line (equation (7)) but the direction of the change in slope is nevertheless an appropriate qualitative measure. For the individual groups of organisms, sample sizes were too small for useful analysis, although they confirmed the same trends as for all species summed.

Sustained Blockage of Drift

A series of interlocking nets (30 × 30 cm) was placed across Jones Creek spawning channel completely filtering all organisms drifting downstream. The blockage was maintained

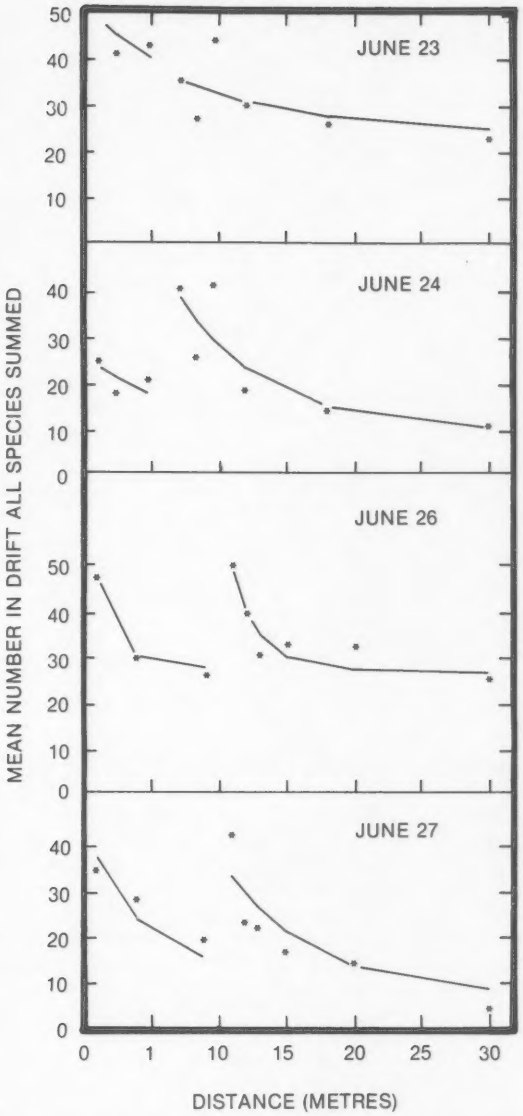

FIG. 4. Lines of best fit for the mean number of drift organisms caught at various distances downstream of two simultaneous disturbances of organisms in the stream bed of Jones Creek, at 0 and 5 m (top two panels) and at 0 and 10 m (bottom two panels).

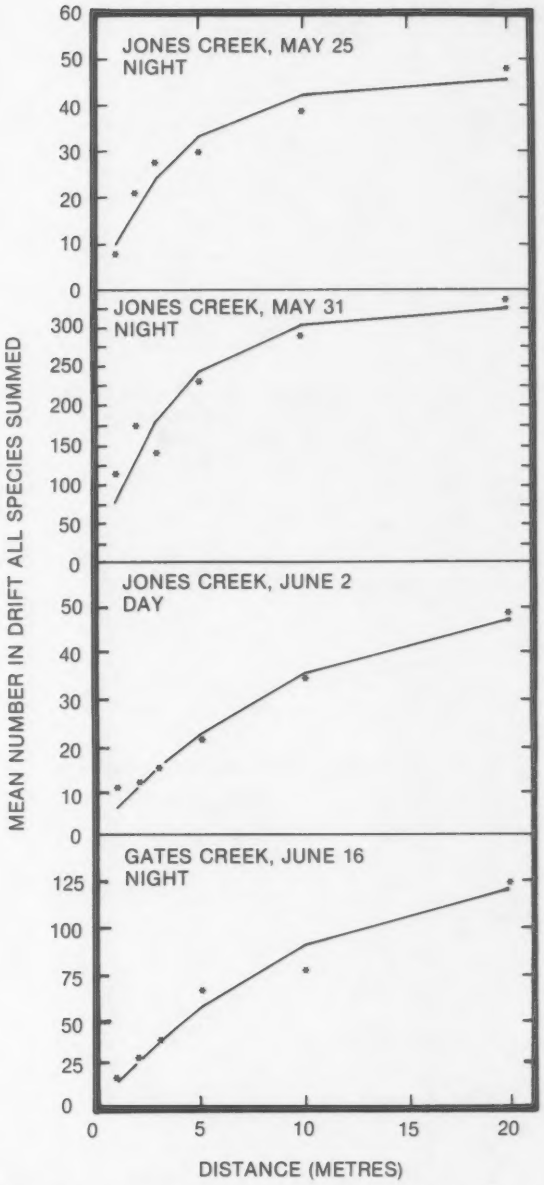

FIG. 5. Lines of best fit for regression on distance of the observed average number of organisms in the drift downstream from complete blockage.

continuously from May 30 to June 9. Each of the blocking nets was cleared every 4 h. Below the blockage, groups of three sampling nets were placed at distances of 1, 2, 5, 7.5, 12, 15, and 20 m downstream. Three control nets were placed 2 m upstream of the blocking nets. The sampling and control nets were in place between 22:50 and 23:50 each day. Differences in velocity at each net, which were relatively small because of the precise control of flow and the uniformity of the stream channel, were corrected to an average velocity, and numbers were expressed as a proportion of the number caught in the control nets.

The analysis was by a routine appropriate to equations (12) and (13). After 4 d, the drift had dropped to a low level with only a slight increase in the number of organisms at various distances below the blockage. The model was accordingly fitted to only the first 4 d of observations.

For each day, the total number of organisms in the drift was higher than predicted at sites closest to the blockage, and on the third and fourth day was lower than predicted at the sites furthest from the blockage, but the fit to the model was otherwise adequate (Fig. 7). The same was in general true for the individual components of the drift, but *Parameletus*, *Paralepto-*

TABLE 5. Observed natural drift and estimates of natural drift, numbers disturbed for each of two disturbances, rate of return, and mean distance travelled for the sum of all organisms in four trials at Jones Creek in which two disturbances were conducted. Mean stream velocity was 0.63 m/s.

Distance between disturbances (m)	Observed natural drift (control nets)	Estimated natural drift, N_{max}	Estimated numbers disturbed		Estimated rate of return to substrate, R	Mean distance travelled (m) X
			N_1	N_2		
5	31	23	27	1	0.1185	8.44
5	15	10	15	53	0.1200	8.33
10	23	27	33	165	0.5354	1.87
10	11	7	35	38	0.1572	6.36

TABLE 6. Observed natural drift and estimates of natural drift, rate of return to substrate, and mean distance travelled for the sum of all organisms in trials in which the natural drift was completely blocked.

Spawning channel	Stream velocity (m/s)	Observed natural drift (control nets)	Estimated natural drift, N_{max}	Estimated rate of return to substrate, R	Mean distance travelled (m) X
Jones (night)	0.62	53	46	0.2560	3.91
Jones (night)	0.54	146	324	0.2661	3.76
Jones (day)	0.77	40	53	0.1079	9.27
Gates (night)	0.36	118	137	0.2139	9.69

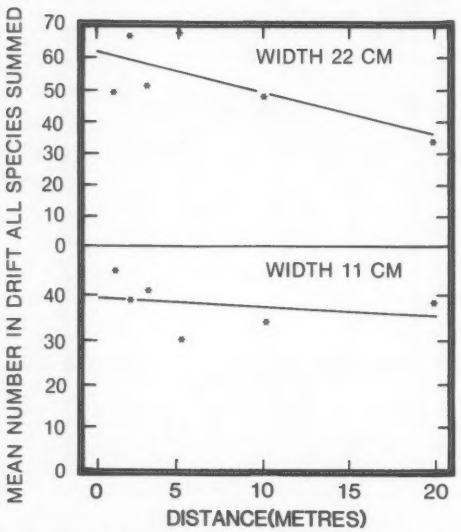

FIG. 6. Lines of best fit for the number of organisms in the drift at increasing distances below a blockage and disturbances of 11 and 22 cm.

phlebia, and *Epeorus* all exhibited a greater abundance than predicted in the drift at sampling stations close to the blockage.

Over the whole experiment, the estimated instantaneous rate of settling from the drift (R) was 0.211, which is within the range found in disturbance experiments. The instantaneous rate of entering the drift (leaving the substrate), which in a natural situation is theoretically equal to the rate of settling, was 0.788, indicating that a much lower proportion of organisms was entering the drift than would be expected.

Three factors could have contributed to this pattern of results. First, there may have been upstream migration of organisms through the substrate, a phenomenon reported by Bishop and Hynes (1969), Elliott (1971b), and for *Parameletus* in particular by Olsson and Söderström (1978). Second, the initial densities of organisms in the substrate were higher immediately below the blockage than further downstream. Third, the decline in the density of organisms in the substrate may have influenced the rate of entering the drift, which has been shown to occur for some stream organisms (Waters 1972; Walton et al. 1977). It may also be possible that there was some leakage of organisms through the blockage but this was thought not to have occurred.

Discussion

The foregoing series of field experiments suggest that the McLay model has considerable utility as a description of the drift process in streams. When the technique of collecting drift is relatively error free, as it can be in our controlled flow channels, the model enables relatively precise evaluation of the distance travelled downstream by organisms that are displaced or enter the drift spontaneously.

Where the predictions of the model were unsatisfactory, unevenness in the distribution of organisms in the stream bed was a likely contributing factor. This was a somewhat surprising feature of this whole series of experiments, for it had been expected that with uniform width, depth, rate of flow, and substrate composition, there would have been a more or less uniform distribution of organisms. It is evidently necessary to make a number of disturbance or blockage observations at

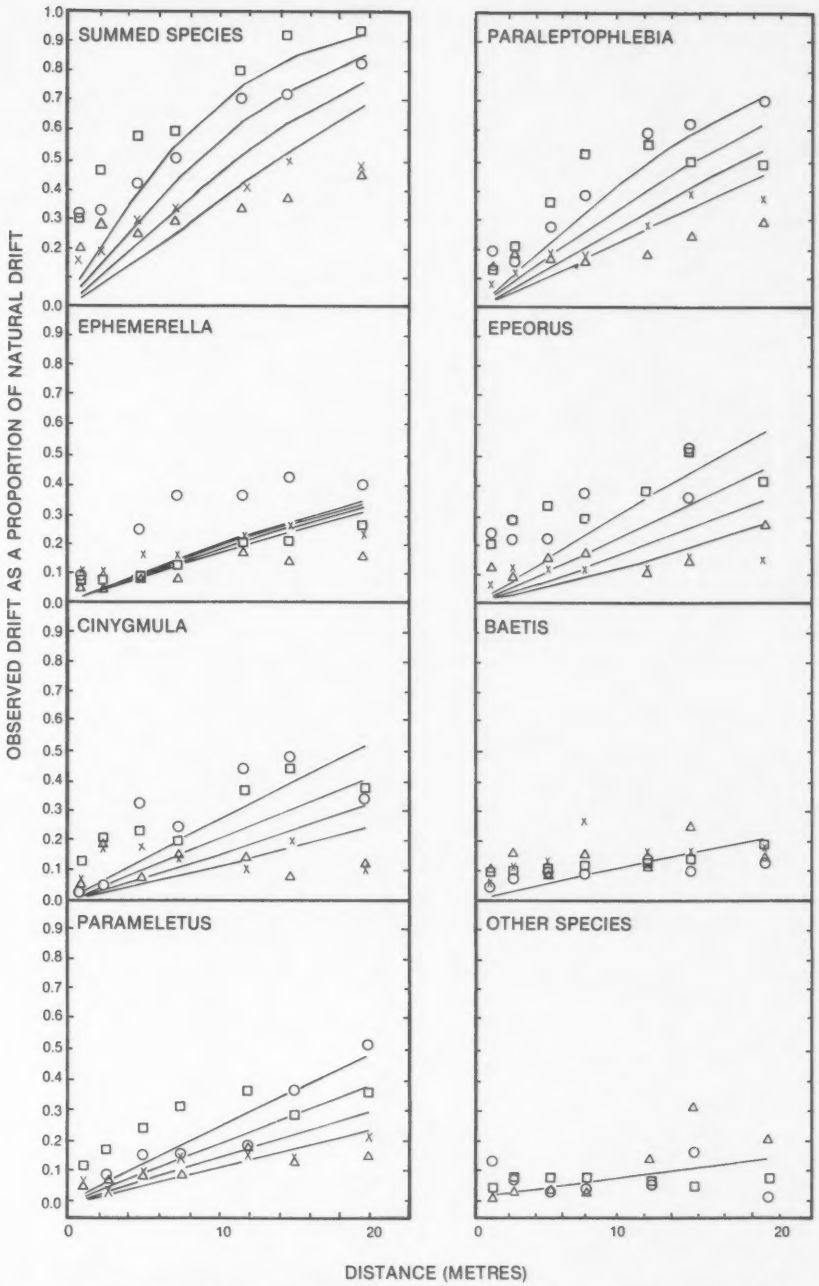

FIG. 7. Observed drift of all species of organisms summed and of various individual genera on four successive days downstream of a sustained blockage. Observed data points: □, first day; ○, second day; ×, third day; △, fourth day. The lines of best fit are, from top to bottom, for the first to fourth days.

various locations on even an ostensibly uniform stream if adequate estimates of stream drift parameters are to be obtained. If interest is centred on relatively uncommon organisms, proportionately more observations would be required. In the series of experiments here reported, it was practical to analyse the data only for those organisms that were predominant in the drift. For the uncommon organisms (or those that were abundant but "undisturbable," such as *Simulium* larvae) it was statistically futile to expect model corroboration or, assuming a model, to expect precise parameter estimation.

These considerations lead naturally to asking why the McLay model should describe the behavior of the aggregate of all

species whether or not it describes the behavior of the individual species or groups of species of organisms. This is not a simple question to address. The relative abundance of various kinds of organisms, their propensities to drift, and the relative average distances they travel would have to be related if there was to be any expectation that in combination they would produce a negative exponential pattern of settling. There seems little reason to believe that things are so tidy, the propensity to drift, for example, being related to a variety of behavioral factors including the tendency to be on top substrate surfaces (Kohler 1983). It seems more likely that, as is often the case, the simple exponential is as good a fit as any to a hodge podge of phenomena and there is little point in trying to be more profound.

Bearing in mind its descriptive utility, it is surprising that the McLay model has not been more widely used to quantify the rate of downstream displacement of stream benthic organisms. Kovalak (1979) used the McLay model to describe the settling process but developed an additional model to describe the process of putting up into the drift and its relation to stream velocity. In part this may reflect the failure of the model, or of any other to date, to relate the number in the drift to the number in the substrate and so to provide a comprehensive model of the changing distribution of the population as a whole. For a single species, with assumptions about the rate of entering the drift in relation to density, such a model can be concocted (equations (10) and (11) are an example in which the rates of entering and leaving the drift are density independent, which has been reported, for example, by Hildebrand 1974 and Ciborowski 1983) but validation would require extensive simultaneous collection of drift and of organisms still in the substrate. In this regard the observations of Townsend and Hildrew (1976) of colonization rates and rates of entering the drift provide the sort of basis on which a more comprehensive model could be made.

If there is virtually no drift below threshold densities, a model will only be useful in describing the dynamics of that part of the population above that density. The failure of the McLay model to predict the numbers in the drift when there is a sustained blockage strongly suggests that this may indeed be the case at least for some species and more complex description of the processes involved may be required.

Acknowledgements

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Movements of Adult Female Dungeness Crabs (*Cancer magister*) In Northern California Based on Tag Recoveries

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Of 11 072 adult female Dungeness crabs (*Cancer magister*) tagged and released in northern California, 463 were recovered with useful location data that could be used for analyses of crab movement patterns. Although qualitative analyses of movement data suggested possible directed northward movement during winter months, application of two nonparametric tests of movement directionality (the Rayleigh test and Moore's test) failed to support significant directed movement during winter. Large numbers of tagged crabs were recovered inshore of release in shallow sandy areas during spring months, but valid statistical analyses of spring movement data were ruled out by concentration of fishing effort in shallow waters during spring. Nevertheless, recovery of large numbers of tagged females in inshore areas during spring is entirely consistent with an hypothesis of spring inshore movement of females for molting, mating, and later extrusion of egg masses. This hypothesis can be constructed on the basis of information independent of tag recovery data. The most striking finding was that 46% of all recovered crabs were recaptured within 2 km of original release sites; many of these crabs had been at large more than 1 yr. Adult female Dungeness crabs appear to constitute extremely localized stocks in northern California.

Des 11 072 crabes dormeurs (*Cancer magister*) femelles adultes étiquetés et relâchés dans le nord de la Californie, 463 ont été récupérés, fournissant ainsi des données utiles sur l'emplacement pour l'analyse des régimes migratoires. Des analyses qualitatives des données sur les déplacements portent à croire à une migration vers le nord en hiver, mais l'application de deux tests non paramétriques de directivité des mouvements (tests de Rayleigh et de Moore) ne l'a pas confirmée. Un grand nombre de crabes étiquetés ont été récupérés au printemps entre le point de lâcher et le littoral, sur des fonds sablonneux peu profonds ; par contre, des analyses statistiques valides des données sur les déplacements printaniers n'ont pu aboutir par suite de la concentration de l'effort de pêche dans les eaux peu profondes au printemps. Néanmoins, la récupération d'un grand nombre de femelles étiquetées dans les eaux côtières au printemps est entièrement compatible avec l'hypothèse d'un déplacement printanier vers le littoral de femelles pour la mue, l'accouplement et la ponte ultérieure de masses d'œufs. Cette hypothèse peut être élaborée à partir de données indépendantes de celles sur la récupération d'étiquettes. Fait frappant, 46 % de tous les crabes ont été récupérés en deçà de 2 km du point de lâcher ; nombre d'entre eux étaient en liberté depuis plus d'un an. Les crabes dormeurs femelles adultes semblent constituer des stocks très localisés dans le nord de la Californie.

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United States Pacific Coast commercial fisheries for Dungeness crabs (*Cancer magister*) prohibit harvest of female crabs. Research efforts have consequently concentrated on commercially valuable male crabs, whereas female crabs have been poorly studied. Migrations and/or movements of male Dungeness crabs have been studied coastwide on the basis of simple, usually qualitative analyses of tag recovery data supplied by commercial fishermen (PMFC 1978; Gotshall 1978; Demory 1971; Jow 1965; Snow and Wagner 1965; Waldron 1958; Butler 1957; McMynn 1951; Cleaver 1949; Spencer 1932). Gotshall (1978) proposed that movements of adult male crabs in northern California were strongly influenced by prevailing currents. He speculated that male crabs move offshore and southward from August to December (during which time the northern California fishery is closed) when the southward flowing California current prevails, and then northward from December through March when the northward flowing Davidson current prevails. This scenario derived in large part from qualitative (nonstatistical) analyses of winter (December–March) commercial fishery tag recovery data that appeared to suggest northward movement of adult male crabs. Directed coastal migrations of Dungeness crabs have been suggested only in localized areas of the Pacific Coast (Waldron 1958; Cleaver 1949), but apparent inshore movements of male crabs have been repeatedly documented (Jow 1965; Butler 1957; Cleaver 1949; MacKay 1942; Spencer 1932) and have usually coincided with annual mating seasons. Gotshall (1978) noted such a trend of inshore movement during the spring (April–May) in northern California, during which time mating takes place. There have been no similar published studies of adult female Dungeness crab movements in northern California or elsewhere along the Pacific Coast.

Mature female Dungeness crabs can be inseminated only immediately after ecdysis while still in a soft-shell condition

(Hartnoll 1969). Polygamous hard-shelled males mate with freshly molted mature females (Butler 1960) in shallow sandy areas (MacKay 1942; Spencer 1932); in northern California, mating occurs in the spring from early April through May (Wild 1980). One might therefore assume that movements of adult male and female Dungeness crabs would be similar, at least during the spring: adult females moving inshore to molt may be "followed" by adult males. However, Diamond (1983) recently found that annual molting probabilities of adult female Dungeness crabs decline precipitously with increasing female carapace width (from about 130 to 155 mm), and that adult females can produce viable egg masses without annual molting and mating. Females are capable of retaining viable sperm for at least 2.5 yr. This new information suggests that not all females may move inshore in spring to molt and mate; those that are not destined to molt may remain offshore. If so, this would imply that size frequencies among recoveries of tagged female crabs might differ between winter and spring periods; relative proportions of smaller crabs might be greater during spring months at inshore locations.

Possible differences between movements of male and female Dungeness crabs or between female crabs of different sizes may be subtle and highly localized. Statistical analyses of directions and distances of movements based on tag recoveries would provide more objective results than those obtained from nonstatistical and qualitative analyses, and are probably necessary for valid inference. However, statistical tests have rarely been used for analysis of tag recovery data, and when they have, they have been simple chi-square tests for independence that cannot quantify direction or magnitude of movements (e.g. see Wespestad et al. 1983, sablefish; Brown and Bennett 1980, European edible crab; Best 1977, Pacific halibut). When quantitative analyses have been used, they have usually consisted of application of Jones's (1959) methods for estimation of directional population velocity and dispersion rates (e.g. Bayliff and Rothschild 1974, yellowfin tuna; Saila and Flowers 1968, American lobster). Unfortunately, these methods are most useful for describing migrations of known highly migratory species, and there are no existing tests with which to measure the statistical significance of estimated directional velocities or dispersion rates. When the existence of directed migrations has yet to be established, these analyses are of limited value and are probably inappropriate.

Studies of avian migrations have produced a substantial literature on directional vector analysis methods (e.g. see Batschelet 1981; Mardia 1972, as cited in Moore 1980). In particular, parametric and nonparametric tests of movement directionality, borrowed from this literature, can be used to determine the statistical significance of apparent movements inferred from tag recovery data (when test assumptions are met). We applied two such alternative nonparametric tests of movement directionality (the Rayleigh test and Moore's modified Rayleigh test) to tag recovery data for adult female Dungeness crabs in northern California to evaluate the possibilities of directed movements during winter or spring periods.

Materials and Methods

Meaningful interpretation of commercial fishery tag recovery data for inference of possible movements or migrations of Dungeness crabs (or other commercial species) should (1) account for or address possible biases due to temporal and spatial distribution of commercial fishing effort, (2) be related to and not contradicted by the life history of the animal as contemporaneously understood, and (3) be based on objective statistical analyses. Few studies of fish movements have met all three requirements, in no small part because the distribution of fishermen (from whom tag recoveries are normally received) cannot be controlled and may seriously depart from an ideal uniform or random distribution. The observation that nonuniform distribution of fishing effort may seriously bias analyses of commercial fishery tag recovery data is by no means new (e.g. see discussions in Bennett and Brown 1983; McKoy 1983; Edwards 1979). However, because rigorous sampling designs to ensure a uniform recovery probability in all directions from release of tagged animals are usually either prohibitively expensive or feasible only on a small localized scale (e.g. see Hyland et al. 1984), a consideration of the distribution of commercial fishing effort is critical for evaluation of most tag recovery data.

The temporal and spatial distribution of fishing effort in the northern California fishery for Dungeness crabs indeed suggests that biases due to distribution of fishing effort cannot be ignored. Intensity of fishing effort is greatest in the first 2 or 3 mo of the fishing season (December–February) during which time fishing effort is distributed fairly randomly from about 18 to 73 m (1 m = 0.55 fathom). Most of a season's harvest of male Dungeness crabs currently takes place during these months. As winter storms subside and swells diminish, fishermen move trap gear into shallower waters until, in the spring mating season, most fishing gear is concentrated inshore along sandy areas at depths of 18 m (10 fathoms) or less (Gotshall 1978). Inshore concentration of fishing effort in spring frequently coincides with a dramatic but short-lived increase in catch-per-trap in what local fishermen call the "beach run". (Methot and Botsford 1982 noted a "large positive deviation in April or May" in catch-per-unit effort in the northern California fishery, but failed to realize its coincidence with the spring mating season at which time relatively dense aggregations of males may be found with molting females.) Thus, for example, if crabs were tagged and released between 30 and 40 m during December, movements of tagged crabs as inferred from commercial fishery tag recoveries would be little biased by distribution of fishing effort during the first few months in which tagged crabs were at large. However, recoveries of tagged crabs during spring months would be seriously biased toward inshore areas due to concentration of fishing gear in those areas.

Tagging and Recovery of Crabs

Capturing, measuring, tagging, and releasing of adult female crabs occurred while on board a contracted commercial crab fishing vessel out of Trinidad Harbor (41°03′N, 124°09′W) during January–February of 1981, 1982, and 1983. Tagging was always completed well before the beginning of the annual spring molting/mating season in early April. Crabs were captured in specially designed traps that were nonselective over adult female crab sizes (Diamond 1983), ≥90 mm carapace width (Butler 1961). Fishing occurred between the mouth of the Mad River (40°55′N) and Freshwater Lagoon (41°15′N) at depths of 18–22 m in 1981 and 1982, and at depths of 22 and 44 m in 1983 (see Fig. 1). Measurements of crab carapace width were taken to 0.1 mm excluding the tenth anterolateral spines. Numbered FLOY anchor tags (model FD68B) were inserted at the posterior epimeral suture to ensure high retention rates through molts (see Poole 1967; Edwards 1965; Butler 1957 for descriptions of previous success with suture tags).

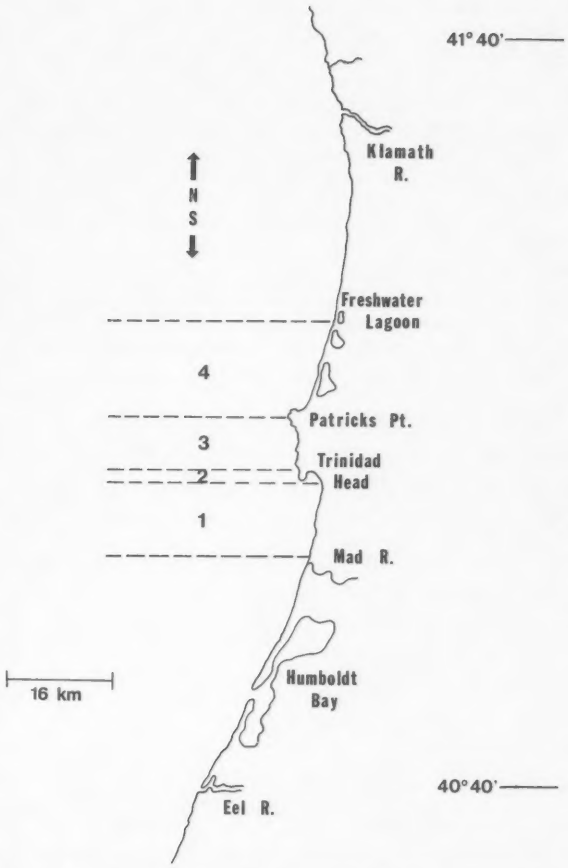

FIG. 1. Study area showing release areas 1, 2, 3, and 4 (see text for physical descriptions of nearshore/coastal habitats).

Commercial fishermen were asked to return tagged female crabs with date, depth, and location (either LORAN-C readings or specific coastal landmarks) of recovery. To encourage return of tagged female crabs, the tag recovery program was well-publicized throughout northern California and southern Oregon, and an annual $500 drawing was held in which one tag was drawn from all those returned during the fishing season; the fishermen who had returned the winning tag received the award. Live recoveries of tagged crabs were not returned to the ocean because tag recovery data were used for purposes in addition to movement analyses, including estimation of survival rates (Youngs and Robson 1975). "Return-to-sea" would have frustrated these additional purposes.

Analyses of Tag Recovery Data

Analyses of tag recovery data were designed to allow evaluation of two distinct possible types of movements: (1) emigration from the release area(s) (which would imply a nonlocalized stock) and (2) seasonal movements within the general release area(s) (which would presume the existence of a localized stock). Because the latter analysis presumed a localized stock, we first examined the possibility of emigration. If crabs did not constitute a localized stock, but dispersed from the release area(s) in a random fashion, then one would expect that distance travelled by crabs would be positively correlated with the number of days at large before recovery (see Skellam 1951). To test this possibility, we calculated the linear correlation between straight line distances from release to recovery and the number of days at large for all recoveries. We found no significant correlation between distance travelled and number of days at large and therefore felt warranted in pursuing seasonal movement analyses.

Analyses of tag recovery data for possible seasonal movements required grouping of recovery data by recovery periods and by release locations. We restricted these analyses to recoveries of crabs during the fishing season immediately following tagging (January–July) to be certain that we would be considering only seasonal movements within a single year. Based on Gotshall's (1978) proposed scenario for movements of male Dungeness crabs in northern California, we isolated two recovery periods as having possibly distinct movement patterns:

(1) Winter: when the strong northward flowing Davidson current prevails (Sverdrup et al. 1942). Winter recoveries included those obtained from the initiation of tagging in each particular year (early January) until March 1. Time at large for these recoveries ranged from about 2 d to 2 mo.

(2) Spring: when offshore winds create upwelled currents (Sverdrup et al. 1942) and when inshore mating occurs. Spring recoveries included those recovered from March 1 through July 31. Time at large for these recoveries ranged from about 1 to 7 mo.

No attempt was made to determine movements during the period August 1 – December 1 when the fishing season was closed.

Winter and spring recovery data were grouped by size at tagging into two categories ($\leq$145 mm carapace width and $>$145 mm carapace width) to allow examination of the possibility that movements during spring depended on whether or not crabs were destined to molt and mate. Diamond (1983) estimated that annual molting probabilities for female Dungeness crabs exceeding 145 mm are less than 10%; molting probabilities are much higher for smaller and younger adult female crabs.

To allow the detection of highly localized seasonal movements, recovery data were also grouped according to four major release areas that corresponded to the following nearshore/coastal habitat types (see Fig. 1): (1) Clam Beach area (40°55′N to 41°01′N): an exposed straight beach; (2) Trinidad Head area (41°03′N): a rocky head that offers northwestern protection to a rocky cove; (3) Trinidad Head to Patrick's Point (41°04′N to 41°09′N): an exposed rocky coast; and (4) Lagoon area (41°10′N to 41°15′N): an exposed straight beach. Data analyses were performed for each area separately and for all areas combined.

Tag recovery data grouped by (a) season of recovery, (b) release location, and (c) size at tagging were subjected first to qualitative visual interpretation of plotted directional vectors from release to recovery locations. Tag recovery data were then subjected, where appropriate, to more rigorous statistical tests based on circular statistics. For all statistical tests, significance level was set at $\alpha = 0.05$.

To apply the statistical tests of movement directionality described below, straight line distances from release to recovery, d, and directions of travel measured clockwise from north, θ, were transformed to rectangular coordinates (x, y) as $x = d \sin \theta$ and $y = d \cos \theta$ for the y-axis oriented northward. (Note, however, that standard trigonometric practice measures θ coun-

terclockwise from a horizontal x-axis so that $x = d \cos \theta$ and $y = d \sin \theta$. Measuring θ from north was adopted because such an angle measurement more directly described movements relative to the northern California coastline.) Because release and recovery data were not considered accurate enough to allow detection of movements ≤2 km, movements of crabs that were ≤2 km were considered negligible and were assigned rectangular coordinates (0, 0) with no polar (d, θ) equivalents.

A single resultant vector of movement (D, Γ) with corresponding rectangular coordinates (X, Y) was calculated by summing the n individual rectangular coordinates (x_i, y_i) within each release area/recovery period:

$$X = \sum^{n} x_i; \quad Y = \sum^{n} y_i; \quad D = \sqrt{X^2 + Y^2};$$

$$\Gamma = \begin{cases} \arccos (Y/D), & \text{for } X > 0; \\ \arctan (X/Y) + 360°, & \text{for } X < 0. \end{cases}$$

If a population were moving randomly, or not at all, individual distances and directions of travel would be expected, on average, to cancel one another and the total average movement, D/n, would be small.

Hotelling's one sample test uses the above statistics to test the null hypothesis that a population is not moving (Everitt 1979; Chase and Bulgren 1971). However, this test assumes that the observed rectangular coordinates (x_i, y_i) form a random sample from a bivariate normal population. The tag recovery data collected in this study failed to meet this assumption. We therefore used two alternative nonparametric tests for movement directionality: the Rayleigh test for randomness (Greenwood and Durand 1955) and Moore's modified Rayleigh test for randomness (Moore 1980; see also Batschelet 1981). The nonparametric tests differ from Hotelling's test in the transformation of the individual movement vectors (d_i, θ_i) to appropriate nonparametric rectangular equivalents. However, all tests share the intuitive argument that, on average, summed transformated coordinates would cancel one another out if there were no directional movement tendency in the population.

The Rayleigh test considers only the individual directions of travel, θ_i, and sets all $d_i = 1$. The resultant vector is calculated as

$$X = \sum^{n} \sin \theta_i; \quad Y = \sum^{n} \cos \theta_i; \quad R = \sqrt{X^2 + Y^2}.$$

The test statistic, $\bar{R} = R/n$, is then compared with the tabulated critical value (Batschelet 1981, p. 339); if $\bar{R}$ exceeds this value, then the null hypothesis of random movement is rejected. (Note that sample size, n, includes all tag recoveries, not just those for which distance travelled is greater than 2 km.) The resultant direction of movement, Γ, is calculated as

$$\Gamma = \begin{cases} \arccos (Y/R), & \text{for } X > 0; \\ \arctan (X/Y) + 360°, & \text{for } X < 0. \end{cases}$$

For Moore's modification of the Rayleigh test (Moore 1980), all directional vectors (d_i, θ_i) are first ranked from least to greatest distance travelled. Letting t_i denote the rank of the ith directional vector, then

$$X = \sum^{n} t_i \sin \theta_i; \quad Y = \sum^{n} t_i \cos \theta_i.$$

The test statistic, R^*, is a measure of the mean distance travelled and is calculated as

$$R^* = R/(n\sqrt{n}); \quad \text{where } R = \sqrt{X^2 + Y^2}.$$

R^* is then compared with tabulated critical values presented in Moore (1980). Resultant direction of movement, Γ, is calculated as above. If distances travelled by crabs were correlated with directions of movement, then Moore's modification of the Rayleigh test would be more meaningful than the Rayleigh test.

Application of both the Rayleigh test and Moore's test requires that detection of actual movement is equally likely in all directions. In the context of tag recoveries from commercial fishermen, this means that fishing effort should be fairly randomly distributed over those depths and areas where recoveries are made. Thus, the two nonparametric tests could be validly applied for winter recoveries over those depths in which crab fishermen fished (about 18–73 m). Valid application of these tests for spring recoveries was clearly ruled out by concentration of fishing effort in shallow waters. We applied these statistics to spring recovery data for comparative purposes only, recognizing that they had no statistical validity (see Discussion).

Results

Emigration

Of 11 072 tagged female crabs released, 463 were returned with useful recapture location information. Of these recoveries, 212 (46%) had moved ≤2 km from the release locations (Table 1), and 272 (59%) had moved ≤5 km from the release locations (Fig. 2). Of the 212 crabs that had moved ≤2 km, 46 (22%) had

TABLE 1. Total numbers of crabs released and recovered in areas 1, 2, 3, and 4 (Fig. 1).

Area	Numbers released	Numbers recovered	Numbers recovered ≤2 km	Numbers recovered >2 km
1	2 765	95	44 (46%)	51 (64%)
2	2 229	75	24 (32%)	51 (68%)
3	2 736	131	50 (38%)	81 (62%)
4	3 342	162	94 (58%)	68 (42%)
1–4	11 072	463	212 (46%)	251 (54%)

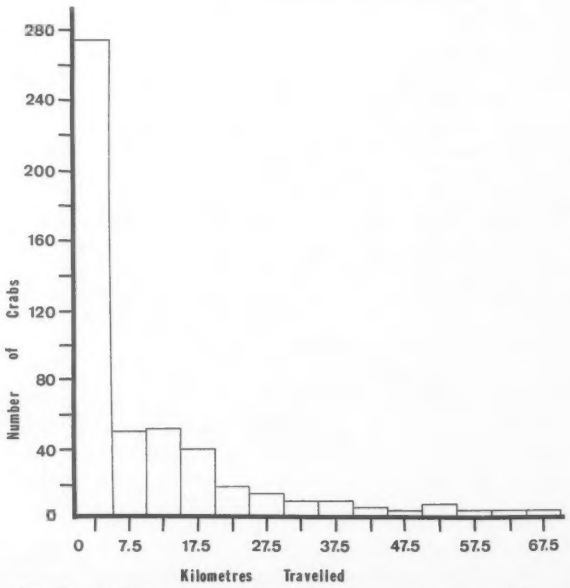

FIG. 2. Distances travelled by crabs before recovery (n = 463).

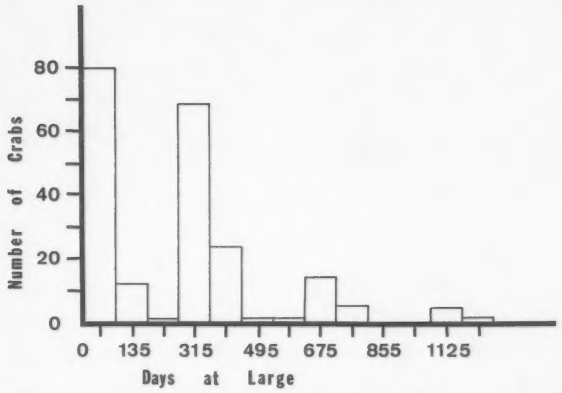

FIG. 3. Days at large before recovery for tagged crabs recovered ≤2 km from release site (n = 212).

been at large more than 1 yr and 10 (5%) had been at large for nearly 3 yr (Fig. 3). Recovery rates were about 10% for adult female crabs tagged at sizes ≥155 mm (the minimum size of full vulnerability to commercial crab trap gear, see Diamond 1983), but were far lower for smaller sized females due to the extreme size selection of commercial gear. Overall recovery rate for all crabs tagged was about 5%. This was quite respectable considering that (a) estimated annual survival rates for adult females ≥155 mm are only about 10% (D. G. Hankin, unpubl. data), (b) commercial harvest of females is prohibited in northern California, and (c) commercial crab traps are designed to allow most smaller females to escape from traps. We found no significant linear correlation between distance travelled by crabs and number of days at large before recovery (r = 0.062); days at large ranged from about 2 to 1300.

Seasonal Movements

A total of 105 crabs were recovered in the winter immediately following release of which 40 (38%) had moved >2 km since release. Plots of individual directional vectors (d_i, θ_i) within each release area showed no obvious dominant direction of movement in any release area (Fig. 4), although 60% of the crabs overall and 75% in area 1 had travelled in a northerly direction (Table 2). A total of 118 crabs were recovered during the spring immediately following release of which 88 (75%) had moved >2 km since release. Plotted directional vectors (for crabs that had moved >2 km) suggested strongly directed inshore and southeasterly movement in area 2, but movements in other areas were less obviously directed (Fig. 5). The absence of recorded movements offshore was striking: 82% of the crabs were recovered inshore of release (Table 3).

Mean resultant vectors (D/n, Γ) were directed northward for three of the four release areas during winter but the mean resultant vector for all areas combined was oriented inshore. In contrast, mean resultant vectors were directed inshore in all four areas during spring months, and average distance of travel was larger than during winter (Fig. 6). (Recall, though, that fishing effort was concentrated in shallow-water areas during spring months.)

Application of the Rayleigh test and Moore's test to winter recovery data failed to reject the null hypotheses of random movement within any individual release area or for all areas combined. Test statistics were nonsignificant in all cases, although there was an apparent qualitative trend of northward movement in area 1.

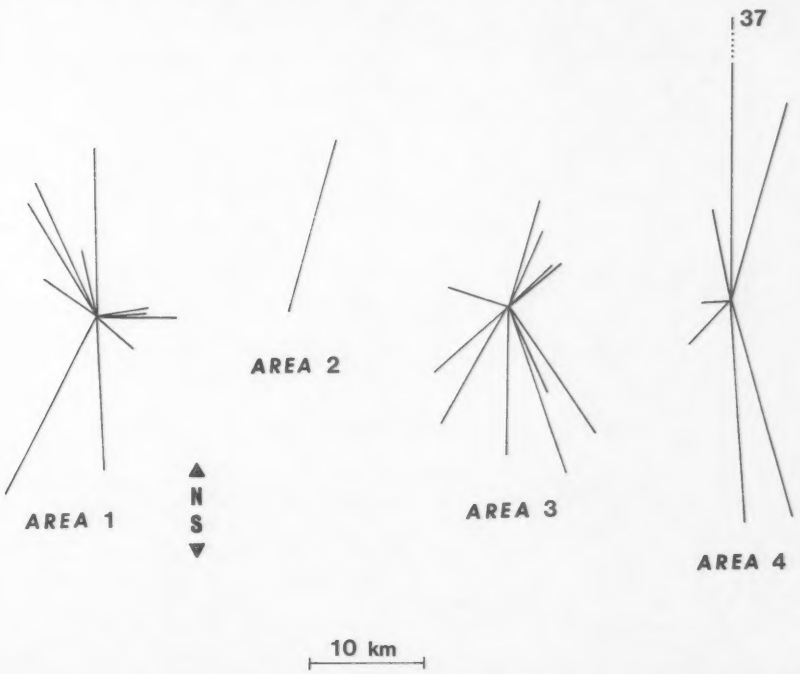

FIG. 4. Movement vectors for individual crabs recovered during the winter period in areas 1, 2, 3, and 4.

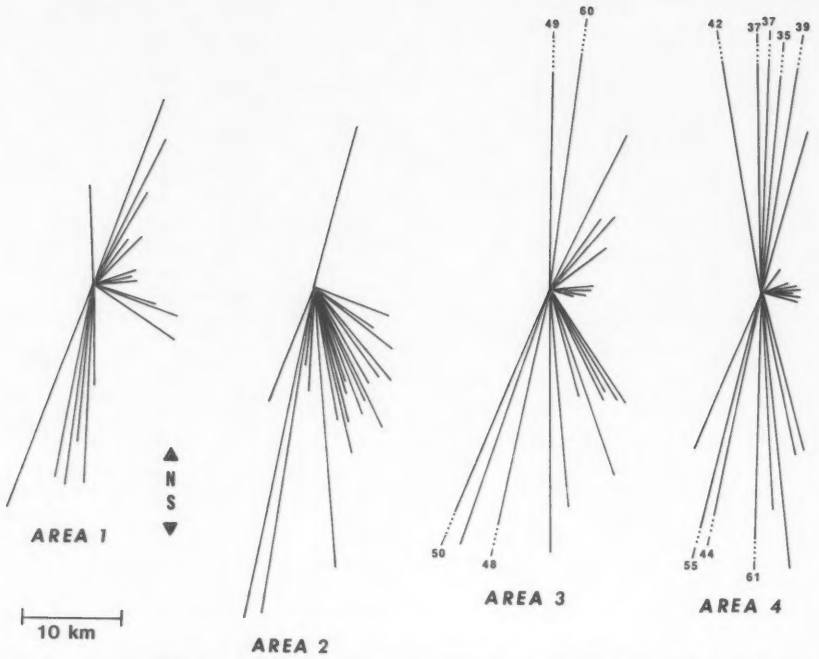

FIG. 5. Movement vectors for individual crabs recovered during the spring period in areas 1, 2, 3, and 4.

TABLE 2. Numbers of crabs recovered north and south of release, or exhibiting no detectable movement (≤2 km), during the winter period in areas 1, 2, 3, and 4 (Fig. 1).

Area	North	South	≤2 km	Total
1	9	3	10	22
2	1	0	6	7
3	9	9	12	30
4	5	4	37	46
1–4	24 (60%)	16 (40%)	65	105

TABLE 3. Numbers of crabs recovered inshore and offshore of release, or exhibiting no detectable movement (≤2 km), during the spring period in areas 1, 2, 3, and 4 (Fig. 1).

Area	Inshore	Offshore	≤2 km	Total
1	18	2	11	31
2	19	2	3	24
3	18	5	1	24
4	17	7	15	39
1–4	72 (82%)	16 (18%)	30	118

Although concentration of fishing effort in shallow sandy areas during spring invalidated application of both the Rayleigh test and Moore's test, results of applying these tests to spring recovery data are presented in Table 4 for comparative purposes. Both tests, had assumptions been met, would have suggested overall southward and inshore movement for all areas combined, and movements within some individual release areas would also have been judged significant.

Movements versus Size

Fourteen crabs tagged at sizes ≤145 mm and 91 crabs tagged at sizes >145 mm were recovered during the winter. Seven (50%) of the smaller crabs and 32 (35%) of the larger crabs had moved >2 km since release. Chi-square contingency tests (Snedecor and Cochran 1980) failed to suggest a dependence of movements of ≤2 km or >2 km on crab size. Twenty crabs tagged at sizes ≤145 mm and 98 crabs tagged at sizes >145 mm were recovered during spring periods. Twelve (60%) of the smaller crabs and 76 (77%) of the larger crabs had moved >2 km since release, and a chi-square contingency test again failed to reveal any dependence of movement on crab size. Movements of both size categories of crabs would have been judged significant and directed inshore on the basis of both the Rayleigh test and Moore's test.

Discussion

Analysis of fish movements on the basis of recoveries of tagged individuals provided by commercial fishermen is clearly not a straightforward task. When fishing effort is fairly randomly distributed, as it was during the winter recovery period for tagged female Dungeness crabs, then the application of circular statistics to tag recovery data can provide an objective method for assessment of movement patterns. This represents a considerable improvement over subjective analyses based on visual inspection of plotted directional vectors or simple chi-square tests. Application of the Rayleigh test and Moore's test allowed determination of the statistical significance of possible winter

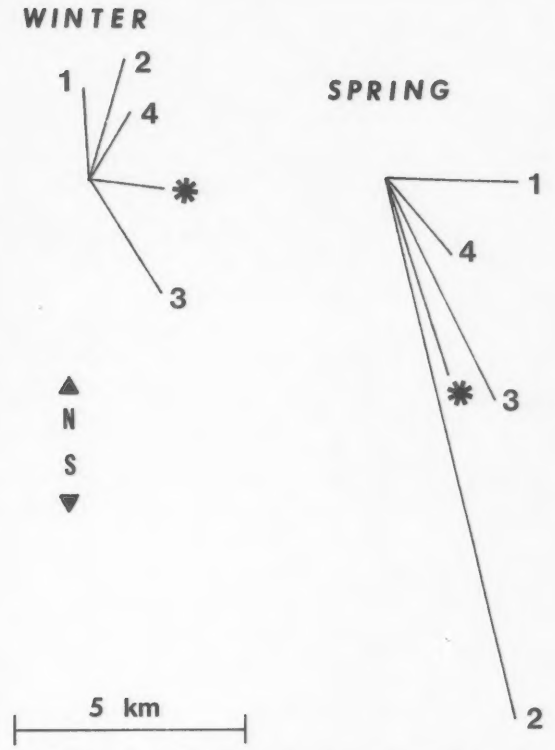

FIG. 6. Resultant mean directional vectors (D/n, Γ) for crabs recovered during winter and spring periods in areas 1, 2, 3, and 4, and for all areas combined (asterisks).

TABLE 4. Rayleigh and Moore's test statistics for spring recovery data. Resultant directions of movement (Γ) are given for movements that were significantly directed (asterisks).

Area	Rayleigh	(Γ)	Moore's	(Γ)
1	0.240	—	0.643	—
2	0.738*	158.3°	1.954*	164.4°
3	0.485*	115.8°	0.964	—
4	0.261	—	0.555	—
All areas	0.352*	124.6°	1.866*	152.7°

movements and, had they exhibited significant directionality, would have allowed calculation of an average distance and direction of movement. If the assumption of bivariate normality had been met, then it would also have been possible to apply the more powerful Hotelling's test for randomness. Based on application of the two nonparametric tests for randomness, we were able to statistically demonstrate an absence of directed movement of female Dungeness crabs during winter. We suspect that if these same statistical tests were applied to data analyzed by Gotshall (1978), they would suggest an absence of directed movement among male Dungeness crabs during winter off northern California. Random, nondirected movement in winter agrees with reports by Jow (1965) and PMFC (1978) for male Dungeness crabs in northern California and southern Oregon.

However, when fishing effort is distributed in a clearly non-random fashion, as it probably is in many cases and as it was during the spring months of this study, it is difficult to interpret the real significance of apparent movements because they are seriously confounded by the distribution of fishing effort. Violation of assumptions for valid application of statistical tests ought not, however, to eliminate a thoughtful consideration of the possible implications of obviously biased tag recovery data, nor ought it to necessarily rule out calculation of statistical measures of distance and direction of travel. For example, had application of the Rayleigh test and Moore's test failed to suggest directed inshore movement during spring, even when tag recovery data were clearly biased inshore, then a reasonable inference would certainly be that crabs did not move inshore during spring (even though test assumptions were violated). More important, however, a consideration of the life history of adult female Dungeness crabs and of the seasonal abundance of adult females in commercial crab traps can aid in interpretation of these biased data.

Female Dungeness crabs must bury themselves at least partially in sandy substrates when eggs are extruded for eggs to develop (Wild 1980), and in northern California, buried ovigerous female crabs are frequently found (sometimes in substantial numbers) in shallow beach areas at low tides during the fall months (October–November) (R. Warner, California Department of Fish and Game, Eureka, CA, pers. comm.). During late December, large numbers of adult female crabs appear in commercial crab traps, just prior to and after hatching of eggs and larval release, when fishing effort is fairly randomly distributed from 18 to 73 m. During spring months, when fishing effort is concentrated inshore on the relatively dense aggregations of male crabs, adult females are frequently captured by fishermen in "premating" embraces. Adult male crabs grasp mature females in these premating embraces just prior to ecdysis of females. These observations suggest a seasonal movement pattern that consists of a spring inshore movement for molting/mating and extrusion of egg masses, and a late fall movement of females offshore for larval release.

Collected tag recovery data, although clearly biased by concentration of fishing effort during spring months, are entirely consistent with the above-suggested movement pattern that is independent of tag recovery data. First, large numbers of adult female crabs were recovered during spring in shallow inshore areas. It is obvious that they could not have been recovered in these areas had they not been present and most of these crabs were recovered well inshore of original release sites. Second, we found no apparent size-dependence among spring recoveries; this might have been expected if those large females that were not destined to molt and mate failed to move inshore during spring. Proportions of large females among all recoveries were not significantly different between spring and winter periods, and the proportion of recoveries that had moved more than 2 km was not less for large females than for small females recovered during spring months. These data are consistent with a need for all adult females, whether destined to molt or not, to seek shallow sandy areas for extrusion of egg masses. And third, recovery of many adult females within 2 km of their original release site during winter, many of which had been at large for periods exceeding 1 yr, suggests that there may indeed be a corresponding movement offshore during late fall. (Alternatively one could argue that most females simply do not move, but the large number of females recovered in shallow waters during spring and the implausibility of crabs not moving for move than 1 yr make this arguement less persuasive.) Thus,

while biases in spring tag recovery data do not allow categorical demonstration of a spring inshore movement pattern for female Dungeness crabs, collected data are entirely consistent with this pattern and with other observations that are independent of tag recovery data but lead to similar conclusions.

Irrespective of the validity of conclusions regarding seasonal movement patterns of adult female Dungeness crabs, the most striking feature of tag recovery data was the high percentage (46%) that was recovered within 2 km of original release sites. This high percentage can, in part, be explained by relatively high recovery rates during the first 2 mo at large so that crabs did not have much time to move in many cases, but more than 20% of crabs that had been at large more than one full year were recovered within 2 km of original release sites. For all practical purposes, given the inaccuracies of release and recovery locations, these crabs had "not moved." This suggests a remarkable degree of "site fidelity" and implies that adult female Dungeness crabs must constitute extremely localized stocks in northern California.

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Model of Sulphate Concentration in a Small Stream in the Harp Lake Catchment, Ontario

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A model previously used for Norwegian catchments was modified to predict discharge and sulphur concentration in a stream draining a small catchment in Ontario. The annual input of sulphur roughly balances the output, the average sulphur flux being about 1.6 g $S \cdot m^{-2} \cdot yr^{-1}$. The average dry deposition was estimated to be about 0.4 g $S \cdot m^{-2} \cdot yr^{-1}$. For good agreement between calculated and observed sulphur concentrations, it was necessary to introduce a reduction (or adsorption) process for sulphate in deeper soil layers during summer and fall. During dry periods, however, sulphate is produced by oxidation in the upper soil layer. The sulphate concentrations in streamwater during snowmelt are remarkably constant. According to model results this could be explained by the existence of a reservoir of easily soluble sulphur in the soil considerably larger than the annual sulphur flux. The basic structure of the models applied to the Ontario stream and to two streams in Norway was the same. It seems likely, therefore, that the model may, with moderate modifications, be applicable to many catchments.

On a modifié un modèle déjà utilisé pour l'étude de bassins en Norvège dans le but de prédire le débit et les concentrations de soufre dans un ruisseau de drainage d'un petit bassin de l'Ontario. L'apport annuel de soufre est à peu près égal à la quantité éliminée ; le flux moyen s'élève à environ 1,6 g $\cdot m^{-2} \cdot an^{-1}$ de S tandis que le dépôt moyen sec a été estimé à environ 0,4 g $\cdot m^{-2} \cdot an^{-1}$ de S. Afin d'obtenir une bonne correspondance entre les concentrations de soufre calculées et observées, il a été nécessaire d'introduire un processus de réduction (ou d'adsorption) du sulfate dans les couches profondes du sol en été et en automne. Pendant les saisons sèches, toutefois, le sulfate est produit par oxydation dans la couche supérieure du sol. À la fonte des neiges, les concentrations de sulfate dans les eaux lotiques sont remarquablement constantes. Selon les résultats obtenus du modèle, la présence dans le sol d'une réserve de soufre très soluble beaucoup plus importante que le flux annuel pourrait expliquer ce phénomène. La structure fondamentale des modèles appliqués au ruisseau ontarien et à deux ruisseaux norvégiens était analogue. Il semble donc probable que le modèle, modérément modifié, pourrait être applicable à de nombreux bassins.

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The causes of the recent acidification of surface waters in several parts of the world, e.g. Scandinavia (Overrein et al. 1980; Swedish Ministry of Agriculture 1982) and North America (Likens et al. 1979; Harvey et al. 1981), are still a matter of considerable controversy. A better understanding of the acidification mechanisms can be obtained by a combination of field studies and mathematical modelling. A complete model would require very extensive information about the catchment (e.g. precipitation, water chemistry, soil chemistry, vegetation). Very few, if any, data sets in existence satisfy these requirements. A modelling effort may nevertheless be worthwhile. In addition to the increased insight obtained, the process may help to plan further field work.

Recently, progress has been made in mathematical modelling of the concentration of important ions in lake and stream water (Schnoor et al. 1982; Chen et al. 1983). Christophersen and co-workers have developed a model for ion concentrations in the streams draining two catchments in Norway (Christophersen and Wright 1981; Christophersen et al. 1982; Christophersen et al. 1983–84; Christophersen et al. 1984). Their model, which requires several years of hydrological and chemical data for calibration, successfully simulated important chemical trends observed in subsequent years in both streams. This does not, of course, prove that the model gives a realistic picture of the processes in the catchments. Confidence in the model would increase if the basic structure could be applied also to other areas. The major objective of this paper is to assess the performance of the model in terms of predicting the hydrological and chemical behavior of a stream draining a small catchment in Ontario. Previous experience with Norwegian catchments had shown that it was necessary to start with a hydrological model because this is the basis for chemical

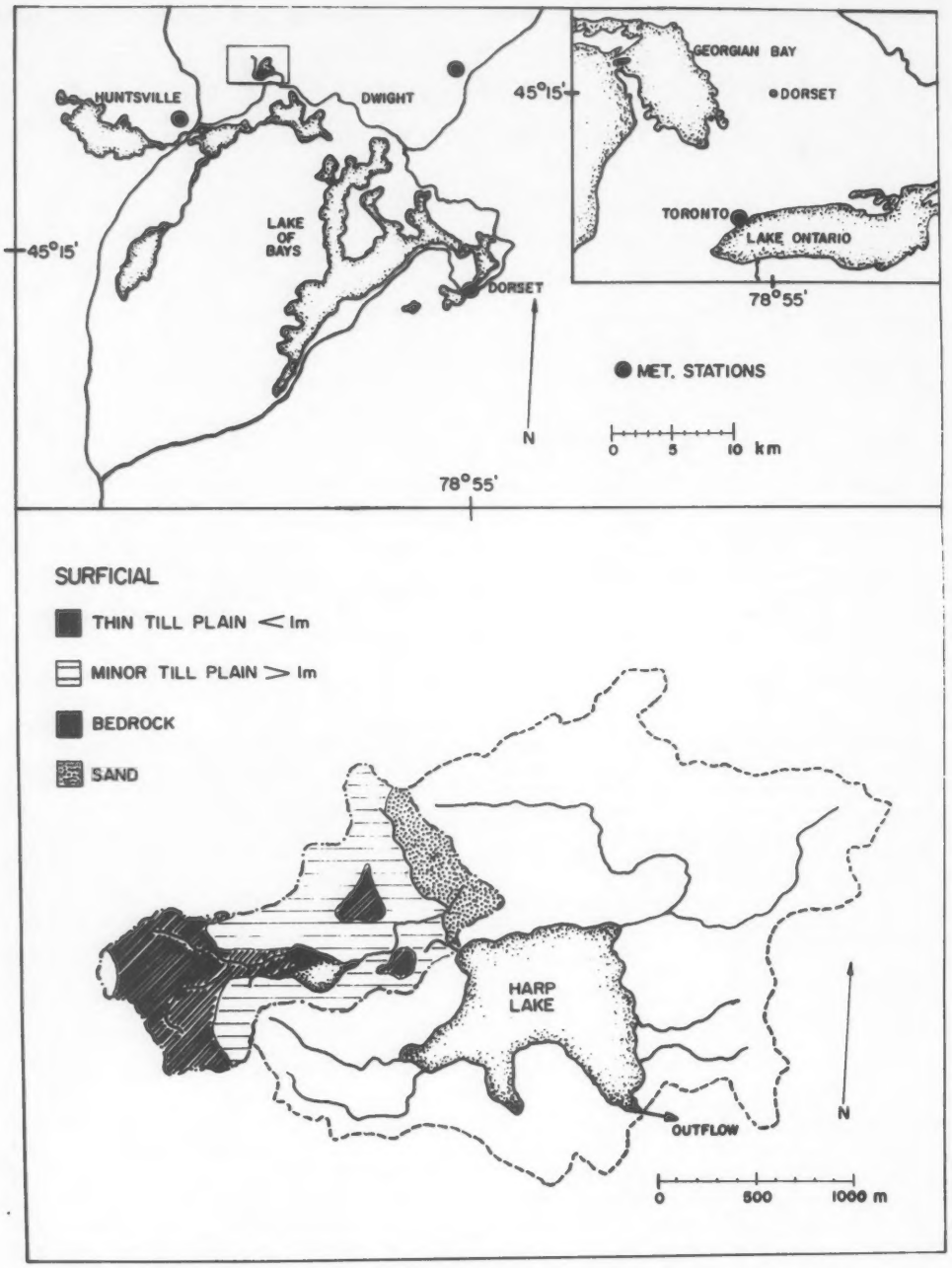

FIG. 1. Location of Harp Lake and the overburden in the Harp Inflow No. 4 subcatchment.

models. Since acidification is undoubtedly linked to sulphate deposition, we considered models of both hydrology and of sulphate concentrations.

Site Description

A tributary (Inflow No. 4) to Harp Lake, 8 km northeast of Huntsville, Ont., was chosen for this study (Fig. 1). This subcatchment has an area of 1.39 km^2 and is almost completely covered with deciduous forest, consisting principally of *Acer saccharum* (sugar maple), *Fagus grandifolia* (beech), *Betula alleghaniensis* (yellow birch), and *Populus tremuloides* (aspen). There are several very small beaver ponds (total area ~3.8 ha) within the watershed. The bedrock underlying most (~87%) of the subcatchment is amphibolite and schist, with a smaller area (~13%) of biotite and hornblende gneiss (Jeffries and Snyder

TABLE 1. Average concentrations of ions and pH in bulk precipitation, Harp Lake Inflow No. 4, and Harp Lake between 1977 and 1983.

	Precipitation	Inflow No. 4	Harp Lake
Alkalinity ($\mu eq \cdot L^{-1}$)	—	79	63
Conductivity ($\mu S \cdot cm^{-1}$)	33	36	35
pH	4.21	6.20	6.31
Ca ($\mu eq \cdot L^{-1}$)	13	153	148
Mg ($\mu eq \cdot L^{-1}$)	4	78	73
Na ($\mu eq \cdot L^{-1}$)	3	55	43
K ($\mu eq \cdot L^{-1}$)	2	11	13
Cl ($\mu eq \cdot L^{-1}$)	4	14	23
SO_4 ($\mu eq \cdot L^{-1}$)	73	167	171
DOC ($mg \cdot L^{-1}$)	0.6	5.1	3.9
Si ($mg \cdot L^{-1}$)	—	4.0	1.5
TP ($\mu g \cdot L^{-1}$)	15.3	16.6	7.8
TN ($\mu g \cdot L^{-1}$)	1030	390	350

1983). The overburden consists of a minor till plain (sandy loam to sand deposits >1 m thick, 56% of the area), with thin deposits (<1 m) and rock ridges covering most of the remainder (33%) of the subcatchment (Fig. 1).

Some aspects of the chemistry of Harp Lake and of Inflow No. 4 have been reported by Jeffries et al. (1979), Dillon et al. (1980), Harvey et al. (1981), Dillon et al. (1982), Dillon (1983), and Galloway and Dillon (1983). The average chemistry of bulk precipitation, of Inflow No. 4, and of Harp Lake is given in Table 1.

The SO_4 concentration in Harp Lake Inflow No. 4 is shown in Fig. 2 for the period 1980–83. Concentrations in three other inflowing streams are also shown for comparison. Although the trends are similar, the fluctuations in SO_4 concentration between sampling dates are generally smaller in Inflow No. 4 than in the other streams.

The concentrations are generally highest in winter and spring. During summer the concentrations tend to be low, but with some high values occurring after dry periods. For example, the very high SO_4 concentrations in Harp Inflow No. 6 in early August of 1981 and 1982 followed 3- and 2-wk periods, respectively, where the stream was completely dry. These peaks probably represent the washout of oxidized sulphur compounds.

Model Description

Modelling of hydrology and sulphate concentrations has previously been carried out for the Birkenes catchment (Christophersen and Wright 1981; Christophersen et al. 1982) and the Storgama catchment (Christophersen et al. 1983–84) in Norway. Snow accumulation and snowmelt were included in only the latter case, and we have therefore taken the Storgama model as our starting point. The hydrological model is depicted in Fig. 3. We consider three reservoirs: one snow reservoir and two soil layers. The upper soil reservoir (A) supplies quickflow, while the lower one (B) provides baseflow. Snow accumulation and melt are difficult to compute from mean daily temperatures around 0°C. We use a "sleet interval" where the precipitation changes linearly from snow to rain as the mean daily temperature increases from 0 to 1.7°C (Christophersen et al. 1983–84). The daily amount of meltwater is computed by the commonly used degree-day method. The fractionation effect observed during snowmelt (Johannessen and Henriksen 1978) is included in the model; i.e. most of the ionic impurities in the snow are found in the first meltwater. (See Appendix and Christophersen et al. 1983–84 for more details.)

Meltwater may be routed directly to the stream or to the upper soil layer. The runoff from the upper reservoir goes either to the lower reservoir or to the stream. The ratio between the two fluxes is determined by the amount of water in reservoir B. An important modification, compared with the model used for Storgama, is the introduction of "piston flow." A part of the water coming from reservoir A pushes out an equivalent amount of water from reservoir B (see Appendix for details). This does not change the simulated discharge pattern, but will affect the chemical composition of the runoff. This modification gives better agreement between observed and simulated concentrations and is also in accordance with hydrograph separations by using environmental isotopes (O^{18}, deuterium, and tritium). Thus, J. D. Bottomly et al. (Natl. Hydrol. Res. Inst., Ottawa, Ont., unpubl. manuscr.) found that storm runoff from the Harp Inflow No. 4 and Harp Inflow No. 5 catchments was composed of 40–90% groundwater depending on rainfall amount and intensity for a few events studied in 1981. M. G. Sklash (The Ind. Res. Inst., Univ. Windsor, Windsor, Ont., unpubl. manuscr.) found that the groundwater component for Harp Inflow No. 4 was more than 85% at peak discharge during an event with about 30 mm of rain (September 17–18, 1982).

The input of sulphur to reservoir A is from wet and dry deposition and from mineralization (oxidation) of compounds containing sulphur in a more reduced form. The latter process will take place mainly in dry periods. At Storgama it was necessary to introduce reduction (or adsorption) of sulphate in the upper soil reservoir during wet periods (Christophersen et al. 1983–84). For the Harp stream this term was not included. The sulphate concentration in discharge from reservoir A is set proportional to the amount of soluble sulphur in the solid phase.

The concentration in the lower reservoir is determined by the equation for dS_b/dt given in the Appendix. The two last terms represent a first-order reaction towards an assumed equilibrium and a temperature dependent-reduction (or adsorption) process, respectively.

In order to assess the performance of the model, the mean observed value for any time period was used as a benchmark model, deemed the best estimate in the absence of any other information. The accuracy of the mean-as-model can be represented as the total sum of squares between the mean and the observed values. The performance of the model can then be assessed by computing a statistic indicating the relative reduction in the total sum of squares about the observations by using the model predictions instead of the mean observed values:

$$(1) \quad P = \frac{\sum_{i=1}^{n} (\bar{x} - x_i)^2 - \sum_{i=1}^{n} (\hat{x}_i - x_i)^2}{\sum_{i=1}^{n} (\bar{x} - x_i)^2}$$

where P is the relative reduction in total sum of squares about the observations, $\bar{x}$ is the mean observed value, x_i are observed values $i = 1$ to n, and $\hat{x}_i$ are predicted values $i = 1$ to n. Where the simulation represents an improvement over the mean observed value model, P will be positive and roughly interpretable like an r^2 coefficient. If the model perfectly simulates observed values, then

$$\sum_{i=1}^{n} (\hat{x}_i - x_i)^2 = 0 \quad \text{and} \quad P = 1.0.$$

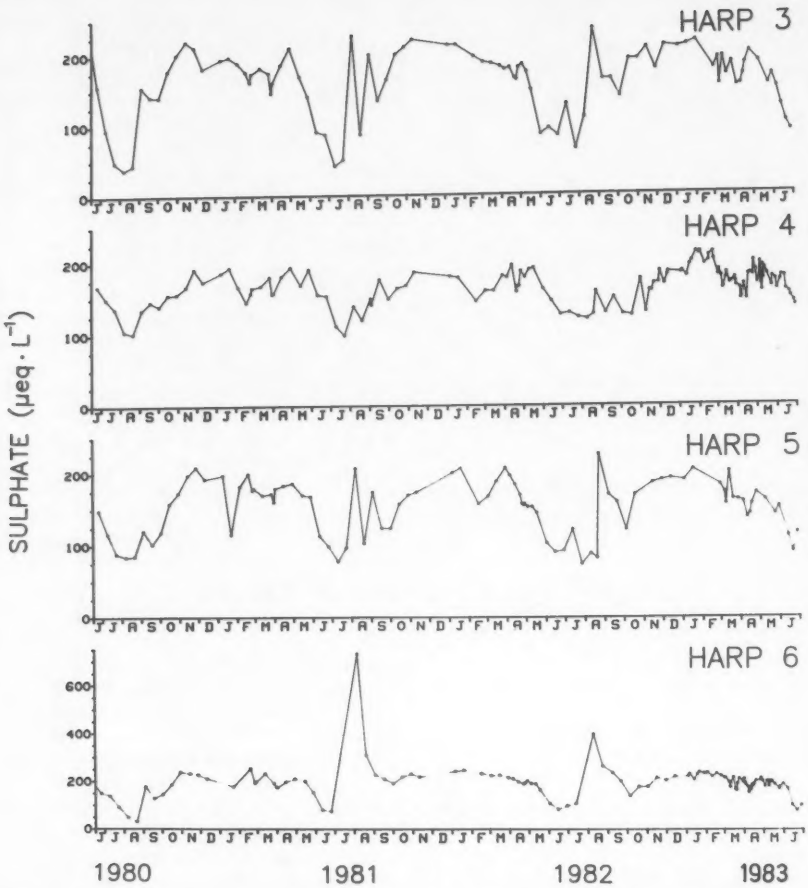

FIG. 2. Sulphate concentrations in four Harp Lake inflow streams for the period June 1980 to June 1983. Points joined by lines for convenience.

Data Base

The data required for the model are as follows: daily mean temperature, daily precipitation amount with sulphate concentration, and average ambient air concentrations of SO_2 and particulate SO_4. Precipitation and precipitation chemistry have been measured in the Harp Lake catchment since 1976 (Scheider et al. 1979). Precipitation gauges are usually less than 100% efficient, particularly during snowfall. These gauge factors are, however, not very well known in this case and we have decided to use the observed values without corrections (cf. Discussion). The chemical composition was determined on samples collected over periods ranging from a couple of days to, in some cases, several weeks. The same chemical concentrations were used for all precipitation events during each period. Since the precipitation chemistry was measured on "bulk" sample (i.e. continuously open collectors), we assumed that some of the particulate sulphate deposited by dry processes was included in this measurement.

Estimates of ambient air concentration of SO_2 and particulate SO_4 were based on daily measurements made in 1981 and 1982 at Dorset, 25 km to the southeast (Lusis et al. 1983; Ontario Ministry of the Environment 1983). Average concentrations of SO_2 in summer (April–October) and winter (November–March) months were 2.1 and 9.2 $\mu g \cdot m^{-3}$ (as SO_2), while concentrations of particulate SO_4 were 3.8 and 2.7 $\mu g \cdot m^{-3}$ (as SO_4), respectively. The deposition velocity of SO_2 was set at 0.8 $cm \cdot s^{-1}$ for the summer and 0.3 $cm \cdot s^{-1}$ for the winter. The former value was used by Christophersen et al. (1983–84), whereas the latter is greater than their value. There is much more vegetation in the Harp Lake catchment than in the Storgama area. However, a smaller deposition velocity during winter than summer is reasonable also in the Harp Lake catchment, since the vegetation is deciduous and there is generally a thick snowpack. The value (0.3 $cm \cdot s^{-1}$) is considerably smaller than the one used by Lusis et al. (1983), but larger than that suggested by Granat and Johansson (1983). For particulate SO_4, we used 0.3 and 0.15 $cm \cdot s^{-1}$ for the summer and winter periods, respectively. These values are low, but it is assumed that some of the particulate SO_4 is included in the bulk deposition. Dry deposition is added to the snow pack when there is snow in the catchment; otherwise it is added to the upper soil reservoir.

Daily temperature was calculated as the average of two readings at Huntsville (8 km west of Harp Lake). Missing values in the Huntsville temperature record were filled with data from Dwight (10 km east of Harp Lake). Comparison of concurrent

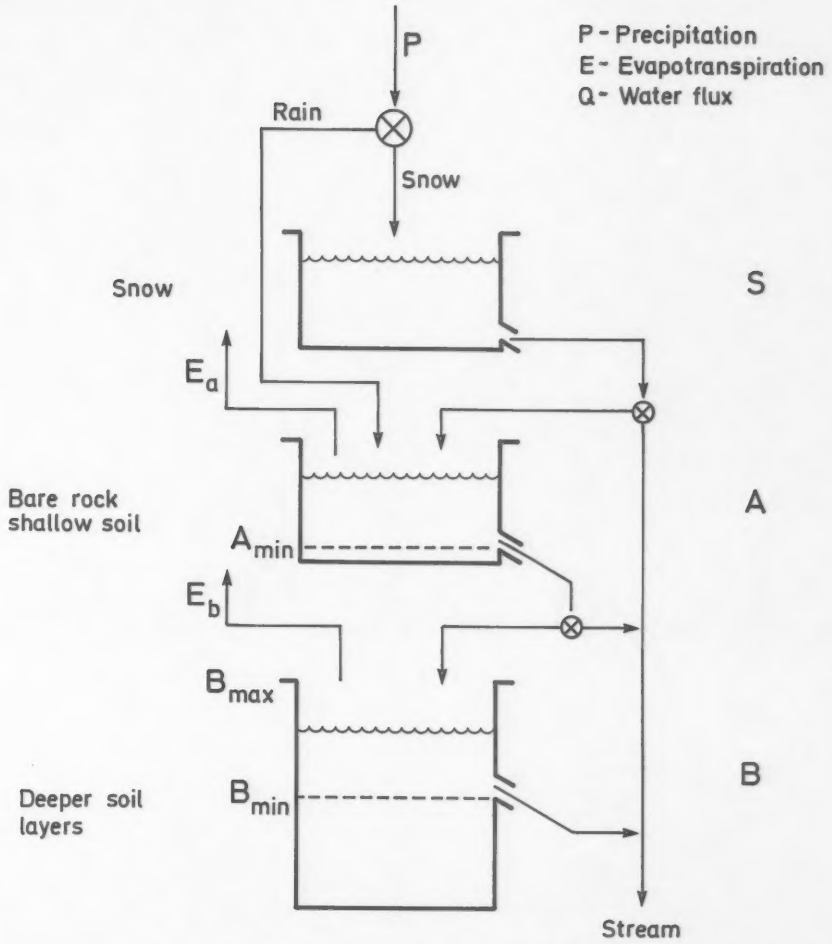

FIG. 3. Hydrological reservoir model.

temperature data for the period January 1, 1976, to December 31, 1982, indicated that values measured at Dwight were 1.5° lower than those measured at Huntsville; this correction factor was applied to any data used from the Dwight station.

Daily discharge was measured for Inflow No. 4 from June 1976 to June 1980 (Scheider et al. 1983). During the construction of a new flume there was a period of about 1 yr with weekly discharge measurements. From June 1981 we usually had daily values, but for some periods, e.g. during snowmelt, there was only weekly observed discharge.

Water samples were taken from Inflow No. 4 for chemical analysis approximately every 2 wk, with sampling during some periods, particularly snowmelt, conducted much more frequently (Jeffries et al. 1979). Until 1980, SO_4 was analyzed by the methylthymol blue (MTB) method (APHA-AWWA-WPCF 1981). Since interference by dissolved organic compounds results in an overestimate of SO_4 concentrations if the MTB method is used (Cronan 1979; Crowther and McBride 1981; Kerekes 1983), particularly in higher colored (dystrophic) water, sulphate was analyzed using ion chromatography (IC) from June 1980. The precision is also much better for the IC than for the MTB method (Crowther and McBride 1981). We corrected the sulphate concentrations for streamwater measured by the MTB method according to equation 2:

$$(2)\quad \text{IC-SO}_4 = \text{MTB-SO}_4\,(0.9 - 0.0025 \times \text{color})$$

where color is measured in Hazen Units. This equation was derived by measuring SO_4 concentration in 30 samples using both chemical techniques. Sulphate concentrations measured for precipitation (always very low color) by the MTB method were not corrected; comparison of results obtained using both methods indicated that there was no systematic difference.

Although Inflow No. 4 was selected for this study, in part, because the color was usually low (average of 35 Hazen Units, 1976–80; $n = 187$), the color on occasion was >100 Hazen Units, particularly in times of very low flow. At these times, the sulphate correction was substantial (35% or greater reduction).

Results and Discussion

Model Calibration and Confirmation

The model was calibrated for the period beginning May 1, 1977, and ending April 30, 1980. Calibration was done by

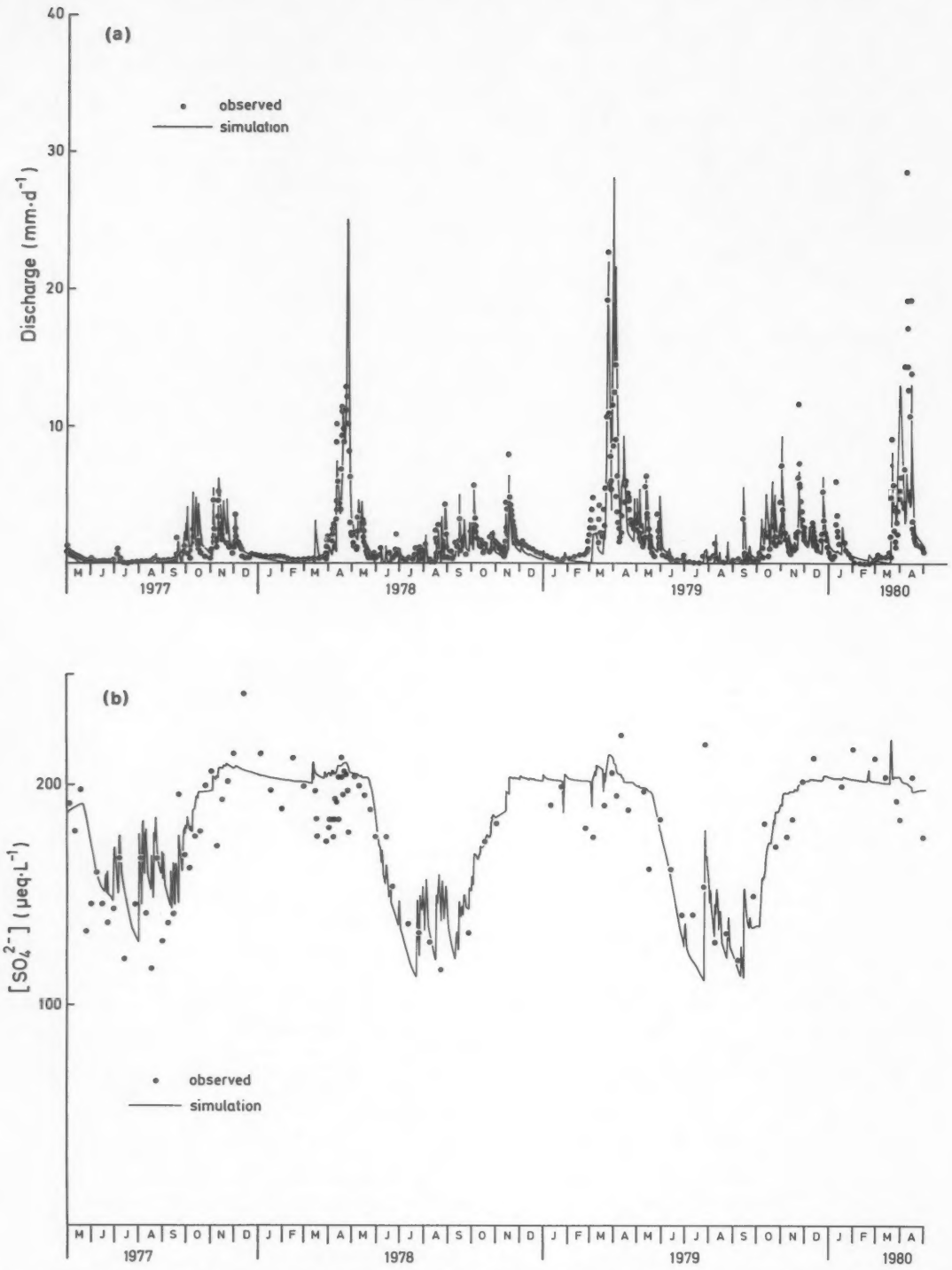
(a)
observed
simulation
Discharge (mm·d⁻¹)
40
30
20
10
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1977
1978
1979
1980
(b)
[SO4 2-] (μeq·L⁻¹)
200
100
observed
simulation
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1977
1978
1979
1980

FIG. 4. (a) Observed and simulated discharge for Harp Inflow No. 4, May 1977 to April 1980 (calibration period); (b) observed and simulated sulphate concentrations for Harp Inflow No. 4, May 1977 to April 1980 (calibration period); (c) observed and simulated discharge for Harp Inflow No. 4, May 1980 to April 1982 (confirmation period); (d) observed and simulated sulphate concentrations for Harp Inflow No. 4, May 1980 to April 1982 (confirmation period).

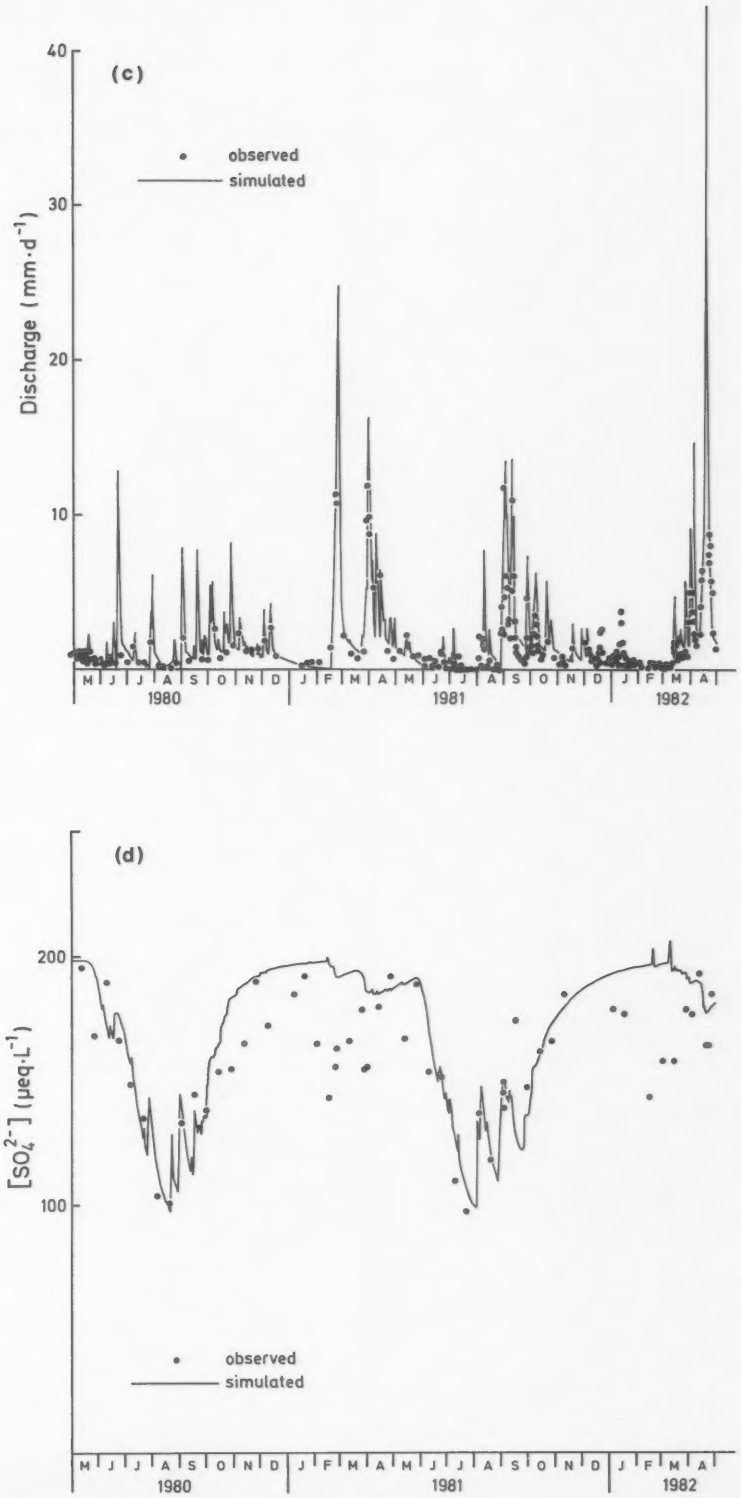

FIG. 4. (*Concluded*)

TABLE 2. Annual precipitation, evapotranspiration, runoff, sulphur input, sulphur output, and sulphur mineralization rate for Harp No. 4 subcatchment.

Period[a]	Precipitation (mm)	Evapotranspiration (mm)	Runoff (mm)		S input ($g \cdot m^{-2}$)[b]	S output ($g \cdot m^{-2}$)		S_{miner} ($g \cdot m^{-2}$)[c]
			Simulated	Observed		Simulated	Observed	
1977–78	887	421	421	381	1.45	1.34	1.18	0.75
1978–79	1024	443	599	631	1.72	1.88	1.84	0.55
1979–80	998	443	571	605	1.63	1.77	1.86	0.58
1980–81	1127	421	698	533[d]	1.66	2.00	1.43	0.42
1981–82	1092	414	676	497[d]	1.73	1.84	1.54	0.48
Mean	1026	428	591	529	1.64	1.77	1.57	0.56

[a]From May 1 to April 30.
[b]The annual dry deposition was estimated to about 0.42 g $S \cdot m^{-2}$. Some of the dry deposition of sulphate was assumed to be included in the bulk deposition (see text).
[c]S_{miner} calculated as described in the text.
[d]Weekly measurements in some periods.

inspection of model predictions compared with observations, with trial and error adjustment of the parameters. Initial values for parameters A, B, and F_a were estimated for 1977 only. A continuous simulation for the interval May 1, 1977, to April 30, 1982, was then carried out without further adjustments of the parameters.

The results of the hydrology simulation for the three calibration years gave $P = 0.52$, indicating that the model explained 52% of the variability that was unexplained by the mean-as-model. A correlation coefficient of 0.80 was calculated between the observed values and the model predictions. For the two confirmation years, $P = 0.44$, indicating a 44% improvement over the mean-as-model. There was a correlation of 0.88 between the observed values and the model predictions. The results of the sulphate simulation over the three calibration years yielded a value of $P = 0.55$ and a correlation of 0.81 between observed and predicted values. For the two confirmation years, the simulated sulphate values gave $P = 0.19$, or 19% better than the mean-as-model, and the correlation between observed and predicted values was 0.78.

Observed and simulated discharge and sulphate concentrations are compared in Fig. 4. The predicted hydrology is generally in close agreement with the measured hydrology. Some disagreement during snowmelt is to be expected, since only mean daily temperatures are used in the model. Furthermore, the temperature was not measured in the catchment, but about 8 km away.

The results for 1981–82 provide the best test of the model, since this year was not used for calibration and daily observed values exist except for short periods. The simulated peak around August 9 is considerably larger than the observed values. Precipitation at Huntsville was about 42 mm on August 4, 13 mm on August 6, and 46 mm on August 7. The simulation results seem fairly reasonable with this amount of rain. Possibly the precipitation in the catchment was somewhat less than in Huntsville in this period. In January 1982 there is no peak in the computed curve even though the observed values indicate increased discharge. The temperature was extremely low in this period, the average for January 10–12 being −27°C. It seems likely, therefore, that the observed values are wrong, probably due to ice formation in the flume.

Simulated evapotranspiration and runoff are given in Table 2. The agreement between simulated and observed runoff is good, with differences ranging from 5 to 10% during the 3-yr calibration period, and about 25% during the confirmation period. With the present database it is, however, difficult to evaluate the model performance with respect to hydrological pathways within the catchment. More measurements of environmental isotopes would be very valuable.

Important trends are also reproduced by the sulphate simulations. The lowest concentrations are found during summer, particularly at low discharge. The model generally predicts an increase in sulphur concentration when the discharge increased during summer because some of the water then comes from the upper reservoir with a sulphate concentration in the range 170–250 $\mu eq \cdot L^{-1}$. The actual value depends on the amount of water-soluble sulphate in the solid phase, F_a. According to the model, F_a varies throughout the year due to accumulation of airborne sulphur, mineralization, and output in discharge (cf. Table 2). The maximum value during summer was found to be between 14 and 26% higher than the value on May 1 of the same year.

The observed values also show a tendency of increasing with discharge during summer and fall, particularly in 1977, 1979, and 1981. There are, however, discrepancies, particularly in late August 1978 and the beginning of September 1980. Clearly, more frequent measurements during some summer and fall events are necessary to evaluate the model in more detail.

The simulated concentrations are an average of approximately 12 and 11% higher than the observed values during the winters of 1980–81 and 1981–82, respectively; the agreement is closer (4–7%) for the winters used for calibration. Since the method for sulphate analysis changed in the summer of 1980, this difference is perhaps, in part, due to inaccurate correction of the concentrations obtained by the MTB method. It may also be related to the differences in goodness of fit in the hydrology submodel between confirmation and calibration periods.

The model allows for the possibility of routing some meltwater directly to the stream. With the constants used (cf. Appendix) the maximum fraction of meltwater with no soil contact is only about 2%. Higher values gave less good agreement.

The seasonal variation in the sulphate concentration shows important differences from that observed at Storgama in Norway (Christophersen et al. 1983–84), particularly during snowmelt. At Storgama there is generally an increase in the

sulphate concentration in streamwater in the beginning of the snowmelt; a pronounced dilution to about one third of the peak value or even less then follows. The concentration of sulphate in the Harp Inflow No. 4, however, shows small variations (Fig. 4). The sum of the amount of sulphur stored in the snow before snowmelt and input of airborne sulphur during snowmelt is 45–71% of the sulphur in runoff during this period (simulation values). The rest of the sulphate must be washed out from the soil, and since the variation in the concentration is small, the sulphate reservoir in the soil must be large. At present we do not have soil data to estimate this reservoir, but samples have been taken in the catchment and analyses are now carried out.

The results in Table 2 indicate that sulphur input to and output from the catchment are roughly in balance. The uncertainty in the observed values for S output may be about 20% due to infrequent concentration measurements, uncertainty in the analyses, and errors in discharge measurements. For the three first years it was necessary to correct the concentration values (see section on data base). On the input side there is considerable uncertainty in the dry deposition values. Average values for ambient air concentrations for the years 1981 and 1982 were used for all years and the deposition velocities may be in error by as much as 50%. This may result in an error of ~15% in the estimated input of total sulphur.

Optimization of Selected Parameters

Selected parameters in the hydrological submodel (A_k, B_k, A_{min}, B_{min}, B_{max}) were calibrated using a technique of nonlinear optimization known as Marquardt's compromise (Marquardt 1963; Draper and Smith 1981). Such a procedure is useful in conjunction with the P statistic (see Model Description), as it optimizes by selecting parameter values that minimize the sum of squared residuals between predicted and observed values:

$$(3) \quad \min \sum_{i=1}^{n} (\hat{x}_i - x_i)^2.$$

We accepted the parameter values at any particular iteration as "optimal" if the relative change in parameter value or the relative reduction in the sum of squares from a previous iteration was 0.0001 or less.

Parameter estimates obtained by optimization of the hydrological model are given as Model II in Table 3. These estimates are considerably different from those used previously (Model I). The very large value obtained from B_{max} is probably not significant. Even with Model I, B_{max} (160 mm) is reached only on a few days each year. The increase in B_{min} is intuitively appealing whereas the low value for A_{min} (5.3 mm) seems less satisfactory from a general knowledge of the catchment.

Since Model I values were used as a starting point for optimization, Model II is by definition better than Model I according to the P statistic (P increased from 0.51 to 0.81 for the calibration period). Closer inspection shows, however, that the main improvements occur during snowmelt. As discussed previously, several assumptions may affect the simulated runoff during this period, in particular the use of the simple degree-day method with the temperature taken as the mean of two daily observations recorded several kilometres from the catchment. Excluding snowmelt, a subjective judgement rather favors Model I. Model II is less efficacious than Model I for the confirmation period ($P = 0.32$). A better optimization could probably be achieved by giving less weight in equations 1 and 3 to the values corresponding to snowmelt. This has, however, not yet been carried out.

TABLE 3. Parameter values for the hydrological submodel (see Appendix) used in most calculations and values obtained after optimization.

	Model I (used to obtain the results in Fig. 4)	Model II[a] (after optimization)
A_k (d^{-1})	0.7	0.5
A_{min} (mm)	15.0	5.3
B_k (d^{-1})	0.04	0.015
B_{min} (mm)	100	189
B_{max} (mm)	160	(984)

[a]The expression for A_{sig} (cf. Appendix) was also modified by optimizing one parameter:

$$A_{sig} = 0.41 - 0.51(B - B_{min})/B_{max} \quad \text{for } B \geq B_{min}$$

$$A_{sig} = 1.0 - 0.59(B/B_{min})^3 \quad \text{for } B < B_{min}.$$

An important result of the optimization exercise is that similar agreement between observed and simulated hydrographs may be obtained with rather different parameter values. More information than can be obtained from the hydrographs is therefore highly desirable in order to get better estimates of the parameter values. To some extent, one may use the concentrations of various ions in streamwater for this purpose. It is preferable, however, to have a satisfactory hydrological model before starting to model the chemistry. Studies to map the details in the water pathways, e.g. by measuring natural isotope ratios, are therefore very useful for improving the present model.

Acknowledgements

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Appendix: Model Details

Hydrology (cf. Fig. 3)

Discharge from reservoir A

$$Q_a = A_k(A - A_{\min}).$$

Discharge from reservoir B

$$Q_b = B_k(B - B_{\min}).$$

If B becomes greater than a given value, $B_{\max}$, we get overflow:

$$Q_{ov} = Q_a A_{sig} - Q_b - E_b.$$

Parameter values used are given in Table 3 (Model I); A_{sig} is explained below.

Evapotranspiration

For T (temperature) < 0°C the evapotranspiration is put equal to zero; for $T > 0$°C we used the following equations:

$$\text{For } A > 0.9A_{\min}: \quad E_a = K_e T, \quad E_b = 0$$

$$\text{For } A < 0.9A_{\min}: \quad E_a = K_e TA/(0.9A_{\min})$$

$$E_b' = K_e T(1 - A/0.9A_{\min})$$

$$E_b'' = 12(B/B_{\min})^2$$

$$E_b = \min(E_b', E_b'').$$

The evapotranspiration should also depend on humidity. To take this into account in a simple way the evapotranspiration was multiplied by 0.65 if the precipitation was ≥1 mm that day. For K_e we used $0.17\ \text{mm}\cdot(\text{°C})^{-1}\cdot\text{d}^{-1}$.

Meltwater routing

The fraction of the meltwater routed to reservoir A is S_{sig}. We have modified the model used for Storgama. A quantity, Froz, is calculated as an indicator of depth of frozen soil. For days where the snow pack corresponds to less than 20 mm of water, we compute

$$\text{Froz} = \text{Froz} + T.$$

Froz is not allowed to be greater than 0°C or less than −50°C. The value of S_{sig} is then computed from

$$S_{sig} = 1 + (\text{Froz}/50)\,(\text{Snoak} - 2\,\text{Smeak})/(K_s\cdot\text{Snoak}).$$

S_{sig} is not allowed to exceed 1. Here, Snoak is accumulated snow and Smeak is accumulated meltwater.

We note that S_{sig} can only be less than 1 before half of the snowpack has melted. If there is not severe frost before a considerable snowpack (water equivalent 20 mm) has formed, Froz will be small and $S_{sig} \approx 1$ also in the beginning of the snowmelt. We used $K_s = 45$.

Routing of water from upper reservoir

This routing is also modified compared with the Storgama model. The fraction routed to the lower reservoir, A_{sig}, is calculated from

$$A_{sig} = 0.75 - K_{as}(B - B_{\min})/B_{\max} \quad \text{for } B > B_{\min}$$

and

$$A_{sig} = 1 - 0.25(B/B_{\min})^3 \quad \text{for } B < B_{\min}.$$

We used $K_{as} = 1.0$.

"Piston flow"

In the original model the water flux $Q_a(1 - A_{sig})$ was routed directly to the stream. In the present work we compute

$$f = 0.1(A/A_{\min})(B_{\min}/B)$$

with the restriction $f < 1$. Further, let

$$Q_a' = Q_a(1 - A_{sig}) + Q_{ov}.$$

The amount routed directly from reservoir A to the stream is then

$$Q_{ac} = fQ_a'$$

while the flux

$$Q_p = (1 - f)Q_a'$$

flows from reservoir A to B and pushes out the same flux with a composition as water in reservoir B.

A storm event with high precipitation intensity tends to give A/A_{min} in the range 2–3, thus increasing f; i.e. more water runs to the stream with a concentration determined by condition in the upper reservoir.

Sulphate Concentrations

Sulphate concentration in meltwater

We simply assume that the concentration in meltwater is three times the average concentration in snow. The somewhat more complicated method used by Christophersen et al. (1983–84) was discarded, since it may give unreasonable changes in meltwater concentrations at days with snowfall during the melting period.

Sulphate concentration in Q_a

$$C_a = F_a K_a = (F_a' - AC_a)K_a$$

where F_a is the amount of water-soluble sulphate in the solid phase in reservoir A and F_a' is the amount of water-soluble sulphate both in solution and in the solid phase (Christophersen and Wright 1981). We used $K_a = 1200\,m^2 \cdot L^{-1}$ and as an initial value (in 1977):

$$F_a'(0) = 235\,000\,\mu eq \cdot m^{-2} = 3.8\,g\,S \cdot m^{-2}.$$

The mineralization (oxidation to sulphate) in the upper reservoir was calculated from

$$S_{miner} = D_{miner}(A'_{min} - A)/A'_{min}, \quad \text{for } A < A'_{min}$$

where $A'_{min} = A_{min} - 3$. We used $D_{miner} = 1050\,\mu eq \cdot m^{-2} \cdot d^{-1}$. The concentration in the discharge from reservoir B was calculated from

$$C_b = S_b/B$$

where S_b is the amount of sulphate in solution in reservoir B. The differential equation for S_b is

$$dS_b/dt = (Q_a - Q_{ac})C_a - (Q_b + Q_p)C_b - E_b C_b + K_b B(C_{eq} - C_b) - S_{red} S_b$$

where Q_{ac} and Q_p have been defined previously, K_b is a rate constant put equal to $0.02 \cdot d^{-1}$, and C_{eq} is an assumed equilibrium concentration in the lower reservoir ($200\,\mu eq \cdot L^{-1}$). S_{red} describes a reduction (or adsorption) process in the lower reservoir. The process is assumed to be temperature dependent. Actually, we should have used the soil temperature. We have, however, assumed that the average temperature for a 20-d period prior to the day considered (T_{av}) will mimic the seasonal variation in the soil temperature. The following function was used:

For $T_{av} \leq 10°C$: $S_{red} = 0$

For $10°C < T_{av} \leq 20°C$: $S_{red} = D_{red}(T_{av} - 10)/10$

For $T_{av} > 20°C$: $S_{red} = D_{red}$.

We used $D_{red} = 0.03$. Note that S_{red}^* gives the fraction of S_b reduced.

Internal Zonations in Sections of Vertebrae from Atlantic Bluefin Tuna, *Thunnus thynnus*, and Their Potential Use in Age Determination

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Internal zonations (bands) were observed in thin sections of vertebrae from 98% of the 200 Atlantic bluefin tuna, *Thunnus thynnus*, we examined between 49.5 and 284.5 cm fork length (FL). These zones occurred in the solid bone area of the sections corresponding to the outer margin of the vertebral cone surface.The remaining area of the section nearest the focus is characterized by spongy bone which obstructs internal zonations associated with early growth history. We present a modified method of determining vertebra age of Atlantic bluefin tuna by adopting a counting procedure which involves enumerating distal internal bands in the sections, as well as proximal external bands on the cone surface to assign ages. Accuracy of this methodology was assessed by evaluating fish where age was known from length frequency and tagging data. The accuracy and precision of estimating age of giant bluefin tuna (≥209.0 cm FL) was improved using our vertebral section method of age determination compared with the more traditional whole vertebra method of ageing. However, results of the vertebral section method in ageing medium tuna (146.0–208.9 cm FL) were inconclusive and this method overestimated age of school tuna (49.5–145.9 cm FL) and should not be used for juvenile age groups. The occurrence of internal zonations in vertebrae of teleosts other than bluefin tuna should be examined as a possible source of age and growth information.

On a observé des bandes internes dans des coupes minces de vertèbres chez 98 % de 200 thons rouges de l'Atlantique (*Thunnus thynnus*) dont la longueur à fourche (LF) variait de 49,5 à 284,5 cm. Ces bandes étaient présentes dans la partie osseuse solide des coupes correspondant au rebord extérieur de la surface conique de la vertèbre. La partie restante de la coupe la plus près du foyer est caractérisée par du tissu osseux spongieux qui oblitère la zonation interne associée au début de la croissance. Les auteurs présentent une méthode modifiée de détermination de l'âge du thon rouge de l'Atlantique à l'aide de vertèbres : il s'agit de dénombrer les bandes distales internes dans les coupes ainsi que les bandes proximales externes sur la surface du cône. La précision de cette méthode est évaluée par l'examen de poissons dont l'âge était connu d'après la fréquence des longueurs et des données d'étiquetage. La précision et l'exactitude de l'âge calculé de gros thons rouges (≥ 209,0 cm LF) ont été améliorées grâce à l'utilisation des coupes de vertèbres au lieu de la méthode traditionnelle par examen des vertèbres complètes. Toutefois, les résultats avec les vertèbres sectionnées n'étaient pas concluants pour l'âge des thons moyens (de 146,0 à 208,9 cm LF) ; de plus, la méthode surestimait l'âge de thons en bancs (de 49,5 à 145,9 cm LF) et elle ne devrait pas être utilisée pour des juvéniles. La présence de bandes internes dans les vertèbres de téléostéens autres que le thon rouge devrait être considérée comme une source potentielle de données sur l'âge et la croissance.

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Accurate and precise estimates of age are essential to understanding the dynamics of fish populations. However, failure to validate the accuracy of age determination procedures has recently been stressed as a serious problem in fisheries and related sciences (Dapson 1980; Beamish and McFarlane 1983; Brothers 1983; Casselman 1983). For example, Beamish and McFarlane (1983) reported that less than 3% of the 500 age and growth papers they reviewed in fisheries journals (dating back to 1915) had validated age determination procedures. One of the most difficult problems is to validate age determination techniques for all age classes in a population (Chilton and Beamish 1982). This is particularly important for long-lived species, such as some oceanic pelagic fishes, where estimating age becomes increasingly more difficult in older fish (Prince and Pulos 1983).

Bluefin tuna, *Thunnus thynnus*, are a relatively long-lived species, with a maximum longevity of more than 30 yr (Mather 1980; Hurley and Iles 1983). This species supports important recreational and commercial fisheries on both sides of the Atlantic Ocean, and attempts to estimate their age and growth rate using skeletal hardparts began in the early 1930s (Sella 1930). However, the only instances where the accuracy of age-

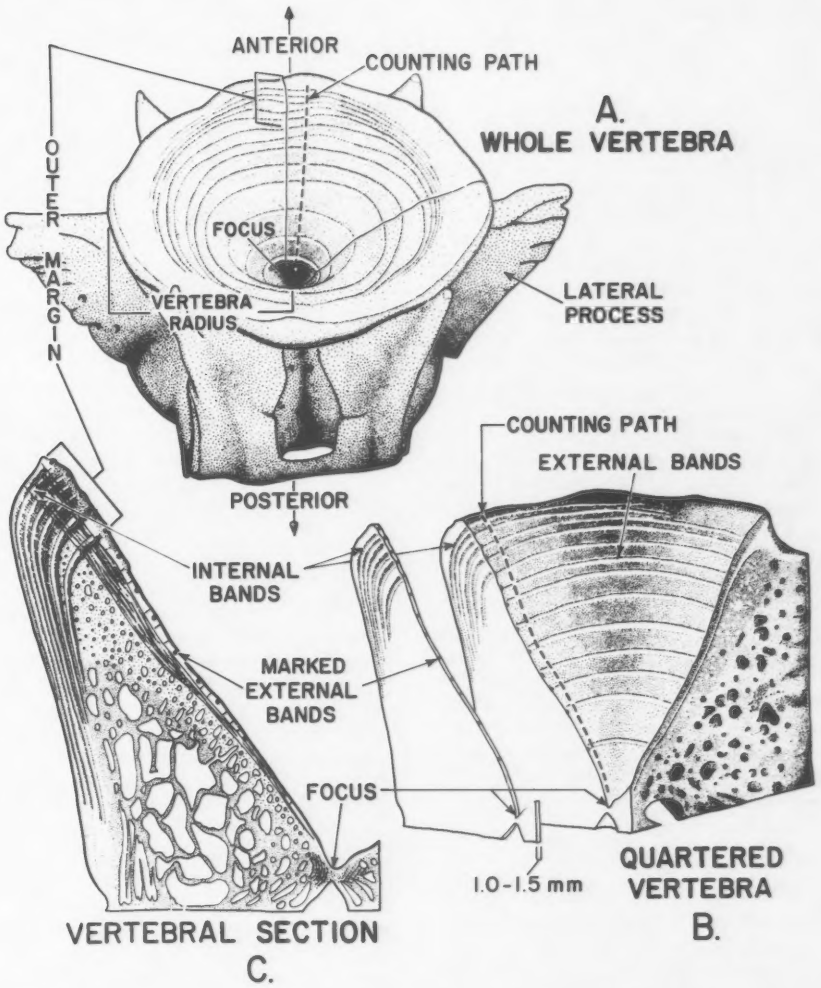

FIG. 1. Schematic diagram of the 35th vertebra from a 227.3-kg (254 cm FL) giant Atlantic bluefin tuna. Internal and external structures and dimensions used for age estimation are given for (A) whole vertebra, (B) quartered vertebra, and (C) vertebral section. (Illustration by J. C. Javech)

ing procedures have been validated are for the first 2 yr of life; validation has never been accomplished for the older age classes (Lee et al. 1983b). Structures used as a source of age and growth information for bluefin tuna include vertebrae, otoliths, dorsal spines, and scales (Westman and Gilbert 1941; Mather and Schuck 1960; Rodriguez-Roda 1964; Nichy and Berry 1976; Compean-Jimenez and Bard 1980; Farber and Lee 1981; Lee et al. 1983a).

Vertebrae are one of the most common skeletal structures used to age Pacific bluefin tuna, *Thunnus orientalis*, as well as Atlantic bluefin tuna (Lee et al. 1983b). However, numerous authors have noted difficulty in interpreting bands on vertebrae (as well as other structures) of bluefin tuna older than ages 6–10 yr (approximate age of first spawn, Baglin 1982). Lee et al. (1983a) reviewed this problem extensively and concluded that vertebral counts tend to underestimate the age of giant tuna (≥209 cm fork length, FL), and the discrepancies appear to be associated with interpreting the crowded bands on the surface of the cone at the outer margin (Fig. 1A).

Based on the analysis of a vertebra from one tag-recaptured giant tuna at large almost 16 yr and whose age was known from tagging records, Lee et al. (1983a) found that the crowded bands in the outer margin should be interpreted as being equal to *at least* 1 yr each. This interpretation, however, still underestimated age known from tagging records by 3 yr. In order to understand this problem better, we examined the internal structure of vertebrae by making a section in the sagittal plane and found that internal bands were evident in the area of the thin sections (0.4–0.8 mm) that correspond to the outer margin or distal portion of the cone surface (Fig. 1A and 1C). In previous studies where vertebrae from bluefin tuna were used as a source of age and growth information, only zonations on the cone surface (external bands) have been used to assign ages. Therefore, our objective was to evaluate the potential of using internal bands occurring in thin sections of vertebrae of Atlantic bluefin tuna for estimating age by (1) determining the extent of occurrence and location of internal bands in vertebrae from all size classes, (2) comparing the precision of counts of vertebral

bands (both internal and external) by two readers from all size classes, and (3) assessing whether counts of internal bands can improve the accuracy of age estimates.

Methods

Vertebrae were collected from United States and Japanese commercial landings and United States recreational landings of bluefin tuna from the Gulf of Mexico, the Florida Straits, and the western Atlantic Ocean from 1975 to 1981. Vertebrae were taken from the caudal peduncle area where sampling would not interfere with commercial processing (Prince and Lee 1982). The 35th vertebra has often been used as a source of age and growth information for Atlantic bluefin tuna (Berry et al. 1977; Hunt 1978; Farber and Lee 1981; Lee et al. 1983a). For consistency and comparative purposes, we also chose the same structure for age determination.

We selected the 35th vertebra from 198 fish from 49.5 to 284.5 cm FL. The fish in this size range were divided about equally between giants (≥209 cm FL) and school and medium tuna (<209 cm FL) to cover the entire size range. Data collected from each fish included fork length, round weight, sex, and date and location captured. Two additional samples were also taken from recaptured tagged bluefin tuna: one giant tuna in 1981 and one medium tuna in 1984.

The terms *precision* and *accuracy* appear frequently throughout this paper and are both important considerations in age and growth studies. To clarify and distinguish their meaning, we define *precision* as a measure of the repeatability, or consistency, of counting concentric bands on the same vertebra and *accuracy* as the proximity of a count, or a mean count, to its true (absolute) value. The degree of repeatability of these age estimates does not necessarily mean that they are also accurate.

Whole Vertebrae

The techniques of Berry et al. (1977) for preparing and staining vertebrae using alizarin red were adopted for our study. The vertebral cone radius (the distance from the focus to the outside margin of the cone) and the band radius (the distance from the focus to the outside edge of each concentric ring) were measured in millimetres. Analysis of the bands on the external cone surface of whole vertebrae followed the general procedures described by Lee et al. (1983a). A counting path was established from the focus to the dorsal edge of the cone surface of each vertebra to standardize counts and measurements (Fig. 1A). External bands on the cone surface appear as alternating bony ridges and valleys. These bands were examined with a stereomicroscope at 6× magnification with reflected light. One measure of the band radii and three counts of the number of bands were made on each vertebra independently by two readers without prior knowledge of fish size. Since there is a positive correlation between size of vertebrae and size of Atlantic bluefin tuna (Lee et al. 1983a), some knowledge of relative fish size was unavoidable.

Precision of counting bands on whole vertebrae and vertebral sections (see next section) by two readers was assessed using the average percent error (APE) approach initially described by Beamish and Fournier (1981) and later modified by Chang (1982). Although APE values were calculated to serve as a basis of comparison with other studies, Chang's index of precision (D) provides the statistical properties of variance for testing the reproducibility of ageing between readers and was adopted for our analysis as follows:

Coefficient of variation (V):

$$(1)\quad V = \frac{\sum_{i=1}^{R} (X_{ij} - X_j)^2}{\frac{R-1}{X_j}}$$

Index of precision (D):

$$(2)\quad D = \frac{V}{R}$$

where X_{ij} = ith age estimate of the jth fish, X_j = average age calculated for the jth fish, and R = number of times each fish is aged.

We tested the null hypothesis that the counts of bands on the same vertebra by reader 1 were equal to counts of bands by reader 2 using the Wilcoxon sign rank test for paired comparisons (two tailed test) and the test statistic D for three size categories: (1) school-size fish (49.5–145.9 cm FL), (2) medium-size fish (146.0–208.9 cm FL), and (3) giant-size fish (≥209.0 cm FL).

Vertebral Sections

Vertebrae were cut with a high-speed saw in the transverse plane (for terminology, see Wilson et al. 1983) to remove the posterior cone and then in the frontal plane across the lateral processes of the anterior cone to isolate that portion of the cone with the counting path and focus (Fig. 1A and 1B). To expose the internal bands, sagittal cross sections of the anterior half of the vertebrae were made with an ISOMET[1] saw using a diamond grit blade to a thickness of about 1.0–1.5–mm (Fig. 1B and 1C). The sections were placed in xylene for 24 h to extract excess oils, allowed to air dry, and mounted on glass slides using FLO-TEX[1] adhesive.

The mounted sections were initially polished to a thickness of 0.4–0.5 mm using 240 grit CARBIMET[1] paper, and a final polishing was applied with 600 grit paper to remove any abrasive marks. The sections were removed from the glass slides by dissolving the adhesive with xylene. Marks corresponding to external bands on the cone surface were made on the face of the sections with a rapidograph pen (Fig. 1B and 1C) by holding the newly cut section contiguous with the quartered vertebra portions. Each section was then remounted on a glass slide and identified by collection number only.

Dry vertebral sections were examined using a stereomicroscope under 6× magnification with transmitted light. An ocular micrometer was used to measure the distance from the focus to each marked external band and the distance from the focus to the distal edge of each internal band. Internal bands, when viewed with transmitted light, appeared as dark opaque zones followed by a light translucent zone (Fig. 1B and 1C). We considered internal bands to be valid and counted them only if they continued along the periphery of the vertebral section (Fig. 1B and 1C). The counting procedure for sections started by including the first externally marked band nearest the focus and continued on a counting path towards the outside margin until the first internal band appeared on the section. At that point, only internal bands were counted (Fig. 2). Thus, the total number of bands in the counts from sections included the

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

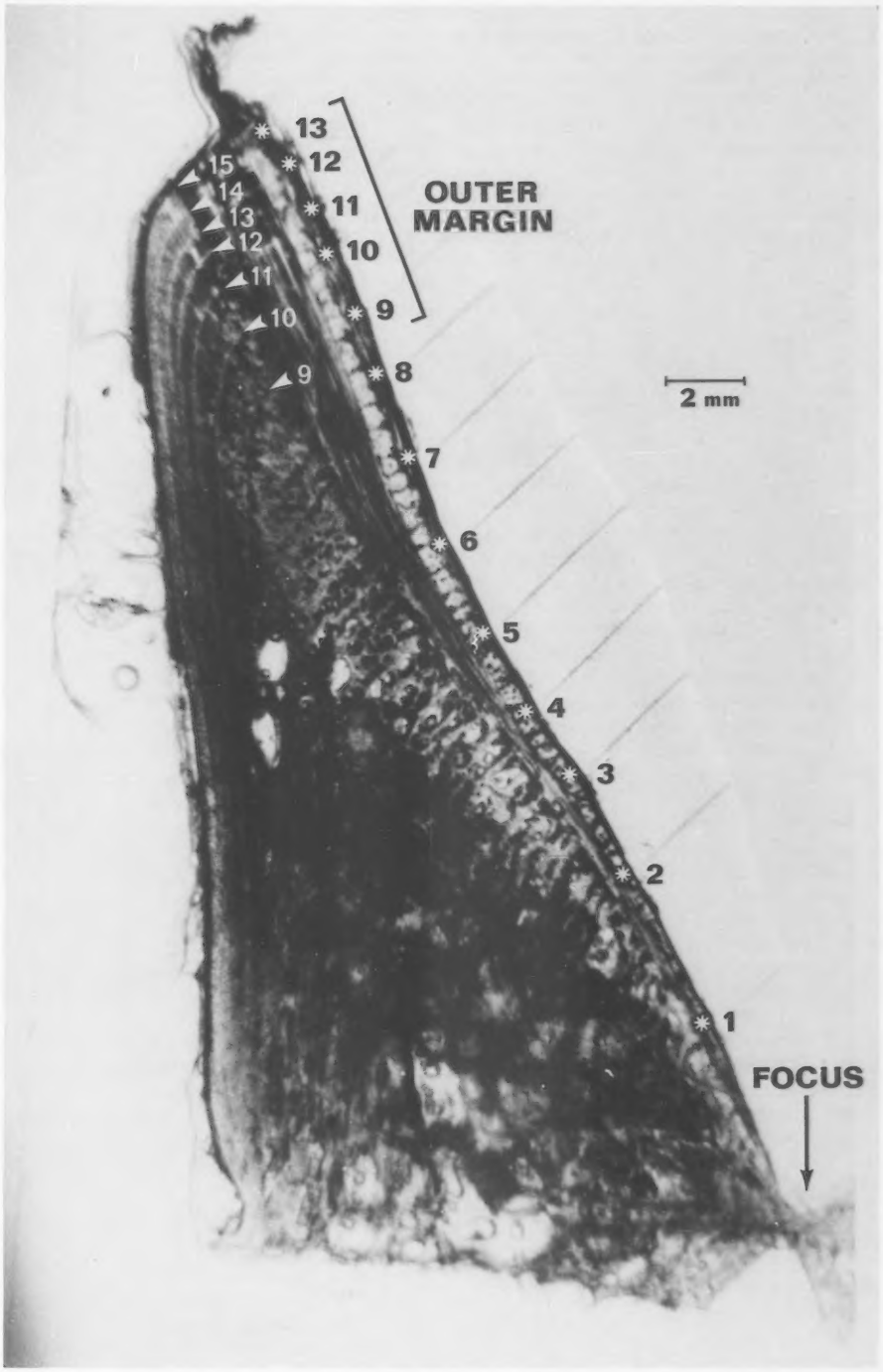

FIG. 2. Sectioned vertebra from a 227.3-kg (254 cm FL) giant Atlantic bluefin tuna viewed under transmitted light. Internal bands (white numbers and arrows), external bands (black numbers and white asterisks), focus, and outer margin are shown as they relate to the whole vertebra (13 yr) and vertebral section (15 yr) methods of assigning ages (see text).

TABLE 1. Comparison of reader precision based on counts from whole and sectioned vertebrae. Sample size (N) and mean values for average percent error (APE), coefficient of variation (V), and index of precision (D) are indicated for each reader and size category. Index of precision (D) of readers 1 and 2 are compared using the Wilcoxon sign rank procedure for paired comparisons for each size category and type of count (whole vertebrae and vertebral sections). Comparisons that were significantly different ($\alpha \leq 0.05$) are indicated alongside mean values of D by an asterisk.

		Reader 1			Reader 2		
Size category (cm FL)	N	Mean APE × 100	Mean V	Mean D	Mean APE × 100	Mean V	Mean D
Whole vertebrae (external bands only)							
49.5–145.9	41	0.30	0.004	0.003	0.83	0.009	0.005
146–208.9	54	3.32	0.034	0.020	4.18	0.047	0.027
>209	103	3.26	0.047	0.027*	4.04	0.071	0.041*
Vertebral sections (proximal external and distal internal bands)							
49.5–145.9	40	4.96	0.037	0.022	6.30	0.057	0.033
146–208.9	54	2.88	0.024	0.014	3.07	0.030	0.017
>209	98	1.78	0.016	0.009	2.25	0.036	0.021

proximal portion of the externally marked bands, as well as all internal distal bands (Fig. 1B and 1C). This procedure was used for each sample, and we evaluated the effect of incorporating internal band counts into our ageing analysis by comparing counts of external bands from the whole vertebrae (Fig. 1A) with total band counts from the vertebral section (Fig. 1C and 2) from the same fish. We tested the null hypothesis that counts of external bands from whole vertebra were equal to total band counts from the vertebral sections, using the Wilcoxon sign rank procedure for paired comparisons, for the same size categories used for analysis of precision given in the previous section.

To determine whether the precision and accuracy of age estimates of bluefin tuna could be improved by incorporating internal bands into the counts, we examined vertebrae from 1- and 2-yr-olds of known age (based on nonoverlapping length frequencies, Mather and Schuck 1960; Parrack and Phares 1979), and vertebrae from one tag-returned giant (Lee et al. 1983a) and one tag-returned medium bluefin tuna (Prince and Lee 1984) where ages (18 and 6–7 yr, respectively) were known from tagging records. Data from the two tag-returned tuna include estimated sizes at release and measured sizes (FL and weight) at recapture. We are confident about estimated sizes at release because biologists did the original tagging in both instances and our experience indicates that size of school tuna can be approximated accurately (more information and discussion of these data are provided in the papers cited above). Data on sex and skeletal structures other than vertebrae could not be obtained from either fish. All methods previously described for making internal and external counts and measurements were also applied to these samples. Results on precision for these samples were compared between readers and accuracy was assessed by comparing whole vertebra and vertebral section age estimates with known age information.

Results

We observed internal bands on the outer margin of vertebral sections from every size (age) category. Sections from 6 of the 200 vertebrae were overpolished and could not be used in our analysis. Only 3 of 194 fish (2%) did not have internal bands; one of these was from a school tuna and the other two samples were from giant tuna.

The area of the outer margin under the cone surface of bluefin tuna vertebrae (Fig. 1C and 2) is represented by solid bone, whereas most of the rest of the internal structure is composed of "spongy" bone with many holes and oil globules. The area of spongy bone near the focus (Fig. 2) obstructs the internal bands associated with the proximal external bands on the cone surface representing early growth history.

Precision

The index of precision (D) for readers 1 and 2 was compared for each size category and type of count using the Wilcoxon sign rank procedure for paired comparisons. The only comparisons found to be significantly different ($\alpha \leq 0.05$) were for the whole vertebra method applied to giant tuna.

The precision of counting internal and external bands on vertebral sections and whole vertebrae, respectively, was inversely related when analyzed by size (Table 1). For example, both readers had the highest precision (i.e. lowest mean values for APE and D) when they counted bands on vertebral sections from giant bluefin tuna and were less precise with school tuna. This trend was reversed when counting bands on whole vertebrae; best precision for both readers in this case was achieved by examining school tuna compared with medium and giant tuna. Reader 1 consistently had better precision than reader 2 for each size category and each type of count (vertebral section or whole vertebra, Table 1), although as stated previously, the difference was significant only for giant tuna on whole vertebra.

Accuracy

We used the whole vertebra and vertebral section methods to estimate age of certain individuals and size categories in the data set where age was known or could be very reliably estimated from independent information (Table 2). Estimated ages were compared with known age data to gain insight into the accuracy of our techniques. The ages of 1- and 2-yr-olds were known because length frequencies of these fast-growing juvenile age groups do not overlap (Mather and Schuck 1960; Parrack and Phares 1979). These data consisted of 9 age 1 (ranging from 49.5 to 67.3 cm FL) and 10 age 2 (ranging from 69.0 to 83.9 cm FL) individuals. The only other known age information was from a giant tuna that was tagged in 1965 and recaptured almost

TABLE 2. Replicate counts of bands for reader 1 and reader 2 on whole vertebrae and vertebral sections from Atlantic bluefin tuna where age is known from length frequency and tagging information. Length, specimen number, and mean counts are also given for each sample.

			Reader 1								Reader 2							
			Whole vertebrae				Vertebral sections				Whole vertebrae				Vertebral sections			
			Replicate count				Replicate count				Replicate count				Replicate count			
Age (yr) based on independent information	Length (cm FL)	Specimen number	1	2	3	Mean count	1	2	3	Mean count	1	2	3	Mean count	1	2	3	Mean count
1	49.5	1	1	1	1	1.0	2	2	2	2.0	1	1	1	1.0	2	2	2	2.0
1	52.0	2	1	1	1	1.0	3	2	2	2.3	1	1	1	1.0	2	3	3	2.7
1	53.0	3	1	1	1	1.0	4	3	3	3.3	1	1	1	1.0	3	4	4	3.7
1	53.3	4	1	1	1	1.0	3	3	4	3.3	1	1	1	1.0	4	4	4	4.0
1	56.5	5	1	1	1	1.0	2	2	2	2.0	1	1	1	1.0	2	3	3	2.7
1	58.4	6	1	1	1	1.0	3	3	3	3.0	1	1	1	1.0	3	3	3	3.0
1	58.4	7	1	1	1	1.0	3	3	4	3.3	1	1	1	1.0	4	4	4	4.0
1	58.6	8	1	1	1	1.0	3	3	3	3.0	1	1	1	1.0	3	4	4	3.7
1	67.3	9	1	1	1	1.0	1	1	1	1.0	1	1	1	1.0	1	1	1	1.0
						1.0				2.6				1.0				2.9
2	69.0	1	2	2	2	2.0	4	4	5	4.3	2	2	2	2.0	5	5	5	5.0
2	70.0	2	2	2	2	2.0	5	5	5	5.0	2	2	2	2.0	5	6	6	5.7
2	73.6	3	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0	3	3	3	3.0
2	76.0	4	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0
2	78.7	5	2	2	2	2.0	2	3	3	2.7	2	2	2	2.0	4	3	3	3.3
2	78.7	6	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0	3	4	4	3.7
2	80.8	7	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0
2	80.6	8	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0	2	2	2	2.0
2	80.0	9	2	2	2	2.0	4	4	4	4.0	2	2	2	2.0	3	3	4	3.3
2	83.9	10	2	2	2	2.0	4	3	3	3.3	2	2	2	2.0	4	2	2	2.7
						2.0				2.93				2.0				3.27
6–7	180.0	1	6	6	7	6.3	8	8	7	7.7	7	7	7	7.0	9	9	9	9.0
18	257.0	1	15	15	15	15.0	18	18	18	18.0	15	15	15	15.0	18	18	18	18.0

16 yr later (Lee et al. 1983a) and a medium tuna tagged in 1980 and recaptured almost 4 yr later (Prince and Lee 1984). Tagging records indicated that the giant was almost certainly 18 yr old, with only a slight chance (≤5%) that it could have been 19 yr old. Tagging records suggested that the medium tuna was probably 6 or 7 yr old.

Readers 1 and 2 correctly estimated ages of 1- and 2-yr-olds using whole vertebrae 100% of the time (Table 2). However, both readers were considerably less accurate in estimating age of these young tuna using vertebral sections. For example, readers 1 and 2 made correct estimates of age 1 tuna using vertebral sections only once out of 9 specimens each and only 3 and 5 times each, respectively, for 10 age 2 specimens (Table 2). Conversely, both readers correctly estimated age (18 yr) of the tag-recaptured giant tuna using the vertebral section 100% of the time and consistently underestimated age of this specimen using the whole vertebra (Table 2). Results from the tag-recaptured medium tuna were inconclusive but generally indicated that mean estimated ages from the whole vertebra for both readers (6.3 and 7.0 yr, respectively) were closer to age known from tagging records than estimated ages using the vertebral section (7.7 and 9.0 yr, respectively).

We made comparisons of band counts for the two ageing methods between readers and size categories of bluefin tuna to provide a basis for assessing the results of these methods for ageing the entire size range. Estimated ages based on vertebral sections were significantly larger ($\alpha \leq 0.01$) than estimated ages from whole vertebrae for every size category. The disparity between the estimated ages from both methods applied to the same fish by two readers is illustrated in Fig. 3. Points below the equilibrium line indicate higher estimated ages using the vertebral section method, and points above the line indicate higher ages using the whole vertebra method. Although these data exhibit considerable scatter for each age class, there is a definite trend towards greater differences between the two methods as age increases. The maximum difference observed between the two methods (over 11 yr) was for a giant tuna of 284.5 cm FL, weighing 454 kg (998.8 lb), and having an estimated age of about 29 yr (Fig. 3).

Discussion

Beamish and McFarlane (1983) equated validating the accuracy of a method of age determination in fisheries biology to standardizing solutions or calibrating instruments in other sciences. They stated emphatically that "all ages for *each* species must be validated." In addition, estimates of the precision of the ageing technique are also necessary because a method must be consistently repeatable for it to be of practical use.

Precision and Accuracy

Many of the percent agreement techniques commonly used in evaluating the precision of a set of age determinations do not evaluate precision equally for all species because these methods

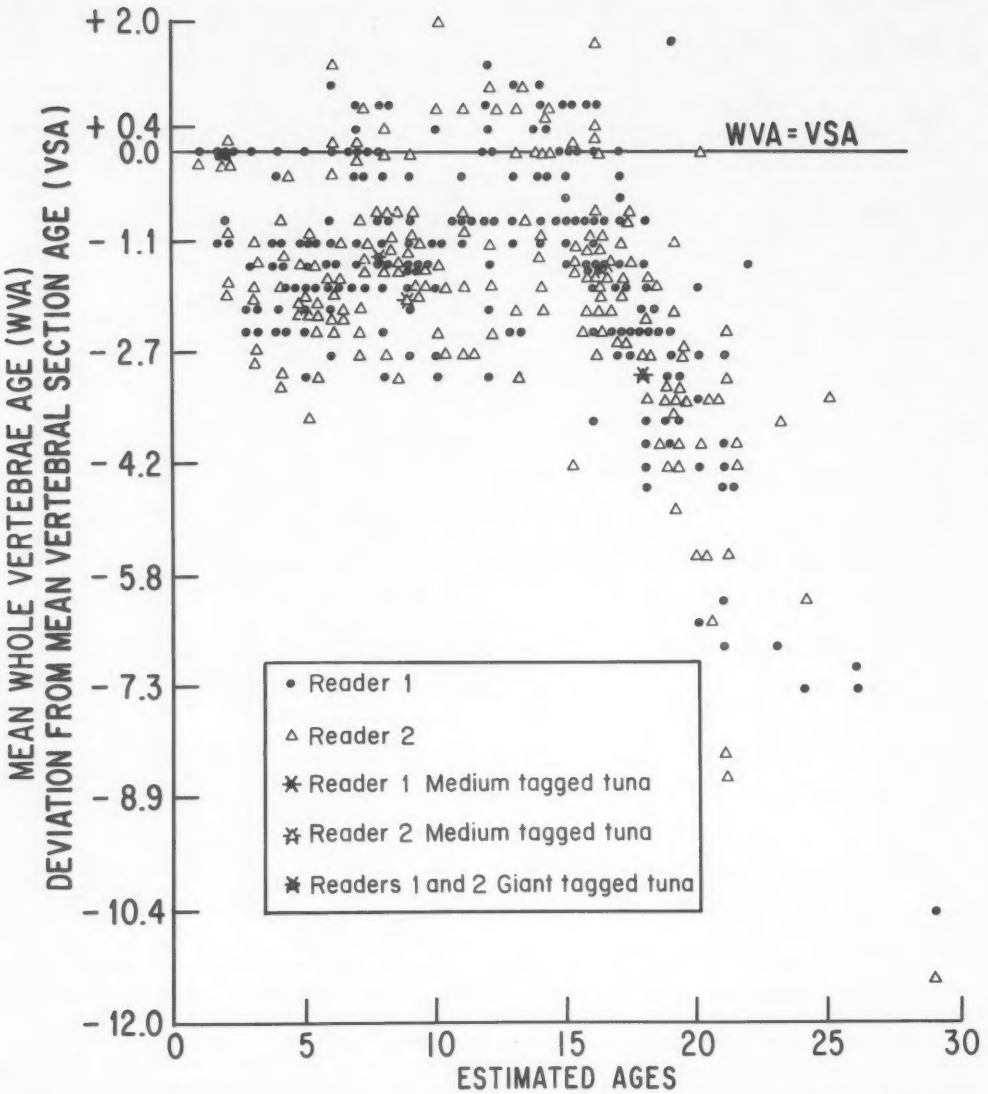

FIG. 3. Deviation of estimating age of 200 Atlantic bluefin tuna using the whole vertebra and vertebral section methods of age determination. Mean estimated age for each method, tagged fish, and reader are based on three replicate counts of bands. Points above the equilibrium line indicate higher estimated ages using the whole vertebra method, and points below the line indicate higher ages using the vertebral section method.

do not take into account the number of age classes in the fishery (Beamish and Fournier 1981). Accordingly, these methods become less meaningful for a long-lived species, such as bluefin tuna, which have many age groups in the fishery. The average percent error (APE) method of evaluating precision offered by Beamish and Fournier (1981) is not independent of age and thus appeared well suited for bluefin tuna.

The 12 mean APE values (ranging from 0.30 to 6.3%) calculated for both ageing techniques from two readers and three size categories of bluefin tuna (Table 1) are within or below the range of APE values published for other species (Beamish and Fournier 1981; Cayre and Diouf 1983). In terms of precision, the newly proposed vertebral section method appeared to have the most utility for ageing giant bluefin tuna, followed by medium tuna, and was least consistent for school tuna. Conversely, the whole vertebra method was most consistent for ageing school tuna and least consistent for giants. Even the lowest rate of precision we found in this study (APE = 6.3%) seems to indicate very good precision, since there are in excess of 20 age groups represented in the Atlantic bluefin tuna fishery (Hurley and Iles 1983). However, these relatively high levels of precision do not necessarily make them acceptable because the level of accuracy of these techniques must also be taken into account. In other words, a very precise ageing technique may be consistently repeatable but if the technique has a low level of accuracy then this could negate its practical

application to fishery problems. Powers (1983) stated that an error rate of 10% or less is an acceptable level of precision when using an ageing technique for stock assessment, but the unstated inference here is that the technique also has an acceptable level of accuracy as well. Therefore, the levels of precision we found for both vertebra ageing methods of Atlantic bluefin tuna fall well below the minimum acceptable precision recommended by Powers (1983) but must also be interpreted in terms of their levels of accuracy before statements can be made about their acceptability.

The findings on the accuracy of our ageing techniques closely paralleled the results of the analysis on precision. For example, the use of the vertebral section method is most accurate (as well as precise) for ageing giant bluefin tuna, based on our analysis of the tag-recapture giant where estimates of vertebral section age agreed exactly with the approximate age of this fish known from tagging records. Accordingly, the vertebral section method, pending further confirmation, could offer a viable alternative to resolving the problem of underestimating age of giant tuna that has been reported in other studies using the whole vertebral method (Mather and Schuck 1960; Rodriguez-Roda 1964; Caddy and Butler 1976; Lee et al. 1983a). Although this conclusion is based primarily on our analysis of the vertebra from one tag-recaptured giant tuna, the unanimous agreement of six independent counts of bands from the vertebral section by two readers (Table 2), with age known from tagging records (i.e. 18 yr), lends strong support for use of this technique for bluefin tuna older than 10 yr. In addition, our analysis of the vertebral section method applied to the entire size range of bluefin tuna (Fig. 3) also corroborates the use of this technique for ageing giants. However, data supporting the use of this technique for size categories other than giant bluefin tuna were not nearly as convincing. (Fig. 3).

The analysis of the vertebra from the tag-recaptured medium tuna was inconclusive because of the wide range in estimated ages (6.3–9.0 yr) between readers using both methods and the overlap of these estimates with the range in age (6 or 7 yr) known from tagging records. Validation of ageing techniques for Atlantic bluefin tuna greater than 3 yr and less than 6–10 yr has not been reported (Lee et al. 1983b), although there is general agreement by numerous authors, using indirect evidence and various methods, on the average size of estimated age classes. However, it should be noted that agreement between numerous unvalidated methods does not in itself constitute validation (Brothers 1983). Thus, the methods used to determine these age groups still await the first evidence of validation according to the criteria stipulated by Beamish and McFarlane (1983) and recently addressed in a workshop on this subject (Prince and Pulos 1983).

We have not been able to formulate an adequate explanation for the apparent overestimation of ageing 1- and 2-yr-old bluefin tuna using the vertebral section method — only 10% of the 1 yr olds and about 50% of the 2 yr olds were aged accurately (Table 2). Internal bands were consistently observed in 1- and 2-yr-old tuna and their lack of association with age may be an artifact of the extremely high rate of growth in these juvenile age classes. Growth of giant tuna, in comparison, is much slower and more consistent from year to year than for juvenile age groups (Hurley and Iles 1983). Therefore, school and medium bluefin tuna should probably be aged using whole vertebrae (or other comparable methods), but the accuracy of this or other methods should be validated by research directed at resolving this problem.

The use of internal bands in sections of vertebrae have not been reported as a source of age and growth information for bluefin tuna or any other teleost to the best of our knowledge. However, Kusakari (1969) observed structural differences between opaque and translucent zones in sections of vertebrae from the flatfish, *Kareus bicoloratus*, but did not actually use sections to estimate age. J. M. Casselman (Ontario Ministry of Natural Resources, Fisheries Branch, Box 50, Maple, Ont. L0J 1E0, pers. comm.) reported that interpreting a combination of proximal external zones and distal internal zones in sections of vertebrae from lake trout, *Salvelinus namaycush*, improved the accuracy of preliminary age estimates for this long-lived species. In addition, numerous authors have used interpretations of zonations in sections of elasmobranch vertebral centra for estimating age and growth rates (Lawler 1976; Tanaka et al. 1978; Gruber and Stout 1983). Thus, from the results from our study we suggest that the internal structure of vertebrae from teleosts other than bluefin tuna should be examined for possible use in age determination.

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Modeling the Lethal Effects of High Temperature on Fish

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We developed a mathematical model relating mean survival times of samples of fish at lethally high temperatures. It permits the estimation of upper incipient lethal temperature (UILT, degrees Celsius) from the results of short-term experiments. Application of the model to data sets obtained from the literature yields "predicted" UILTs usually within 0.5° and almost always within 1° of observed values. The model was also applied to determine threshold toxicities (LC50, 144 h) of copper ion from tests of shorter duration.

Les auteurs ont élaboré un modèle mathématique du temps moyen de survie de poissons échantillonnées en présence de températures létales élevées. Ce modèle permet d'estimer la température létale initiale supérieure (TLIS) à partir des résultats d'expériences à court terme. L'application du modèle à des ensembles de données tirées d'ouvrages publiés a produit des TLIS généralement en deçà de 0,5°C et presque toujours en deçà de 1°C des valeurs observées. Le modèle a aussi été appliqué pour déterminer les toxicités seuils (CL50, 144 h) d'ions de cuivre dans des expériences de courte durée.

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Two main methods describe quantitatively the acute lethal effects of high temperature on fish. In the first, samples of fish are exposed to gradually increasing temperatures; observations consist of temperatures at which signs of acute distress, i.e. loss of equilibrium or cessation of opercular movements, become evident. In the second method, samples of fish are transferred directly to baths maintained at constant temperatures and percentage mortality or time to mortality recorded. Details of both methods and their relative merits are discussed by Fry (1967). Our objective was to examine mathematical models related to the second method; we focused on a model that permits predictions of threshold lethal temperatures (degrees Celsius) from the results of short-term experiments.

For the purposes of describing the lethal effects of temperature on fish, the upper part of the temperature scale may be divided into three zones (Reynolds and Casterlin 1979). The highest of these is the zone of thermal resistance; in it, fish succumb to thermal death within relatively short periods of time, depending on the actual temperature. Below this zone is the zone of thermal tolerance, in which high temperature is not the direct cause of death. These two zones are separated by a transitional band about 1° in width. Temperature is not lethal at the lower extreme of this band but mortality may be considered complete at the upper boundary. The upper incipient lethal temperature (UILT) lies between these two limits and is defined as the temperature at which 50% of the population survives an indefinitely long exposure (Fry 1947). This statistic is analogous to the LC50 of toxicological bioassays where temperature corresponds to the lethal identity.

In the method of abrupt transfer to constant temperature baths, the choice of bath temperatures is crucial. In practice, a series of bath temperatures is selected so that death occurs in a relatively short time at the upper extreme and not at all at the lower. For bath temperatures in the zone of thermal resistance, individual times to death of each fish in the sample are recorded, and either the median time to death or its close estimate, the geometric mean (Doudoroff 1942, 1945; Fry et al. 1946; Brett 1952), is calculated. The relationship between time to death and temperature is the central object of our study.

A typical relationship between temperature and median time to death is shown in Fig. 1A. Generally the experimental curve is approximately hyperbolic in form, with one arm of the curve apparently asymptotic to the UILT. Traditionally the data have been transformed to obtain a straight line fit by taking the logarithm of the median time to death (Doudoroff 1942, 1945). This procedure assumes that the original data are described by

$$(1) \quad t = Ke^{-cT}, \quad T \geq T_c$$

where t = median time to death, T = bath temperature, K and c are constants, T_c = UILT, and e is the base of the natural logarithms. Assuming model (1), it follows that

$$(2) \quad \log t = \log K - cT, \quad T \geq T_c$$

so that the logarithm of the median time to death depends

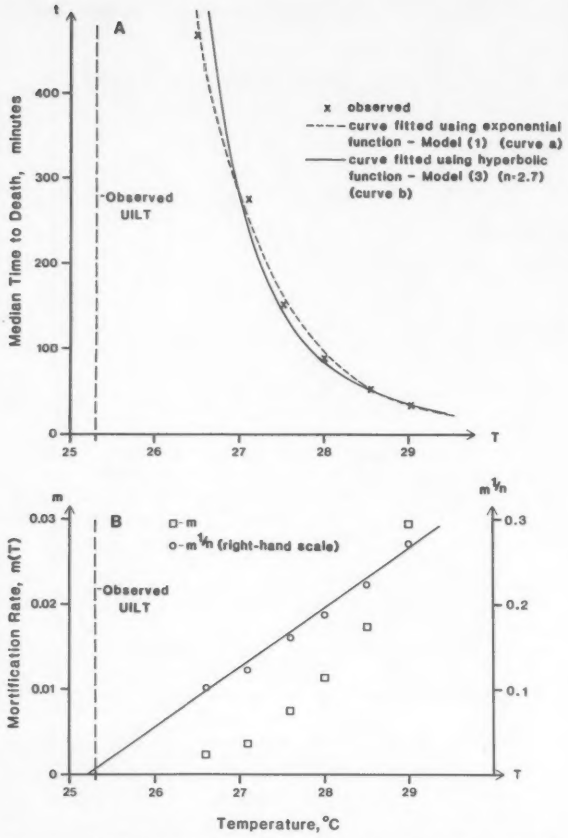

FIG. 1. (A) Relationship between median time to death and lethal temperature as described by models (1) and (3). Data obtained from brook trout acclimated to 15°C (Fry et al. 1946). (B) Linearization using the parameter n of the relationship between mortification rate, $m = m(T)$, and lethal test temperature, T. Data as in Fig. 1A.

linearly on the bath temperature. This straight line segment terminates abruptly at $T = T_c$. Curve a in Fig. 1A is derived from the data of an actual experiment by fitting (2) to determine K and c and then inserting these values in (1). Note that the vertical line $T = T_c$ is not, in fact, asymptotic to graphs arising from (1).

Development of New Model

The new model we propose replaces (1). It posits a relationship between temperature and median time to death in the zone of thermal resistance which includes, in a natural way, the UILT as a parameter. Consequently, close estimates of the UILT can be obtained using data only from the zone of resistance. Furthermore, the model can aid in the selection of a bath temperature series, making the study of the upper lethal temperature relations of a species more economical and efficient.

The lethality of a test temperature in the zone of resistance is usually expressed as the median time to death. Its reciprocal, the mortification rate (Fry et al. 1946), has been ingeniously used to predict the cumulative lethal effects of a fluctuating temperature regime from the results of constant temperature experiments. For a (constant) temperature at which the median survival time is 100 min, for example, the mortification rate is 0.01/min. Since the mortification rate in the zone of thermal tolerance is, by definition, zero, extrapolation of the curve of mortification rate downward to intersect with the temperature axis should provide a good estimate of the upper limit of this zone, i.e. a temperature slightly below the UILT. Unfortunately, however, experimental data generally indicate that mortification rate is not a linear function of temperature, making it difficult to accomplish the desired extrapolation with accuracy. This situation is illustrated by the mortification rates derived from the data in Fig. 1A, which are shown (open boxes) in Fig. 1B.

Focusing on the mortification rate uncovers a serious flaw in model (1). This model implies that the mortification rate $m(T)$ satisfies

$$m(T) = \frac{1}{t} = K^{-1}e^{cT}, \quad T \geq T_c.$$

In particular,

$$\lim_{T \to T_c} m(T) > 0$$

so that data represented by (1) cannot be extrapolated to zero mortification rate. For this reason, other models of the relationship between median time to death and test temperature were investigated. The general form

$$(3) \quad t = \frac{k}{(T - T_c)^n}, \quad T > T_c$$

was found to be particularly useful. Here, k and n are constants. (Equation (3) has been used previously for modeling related phenomena. See Coutant 1972.) It is evident that (3), like (1), is a three-parameter model, but that the restriction $T > T_c$ arises naturally in (3). The vertical line $T = T_c$ is, in fact, asymptotic to the curve of (3).

The problem of fitting experimental data to (3) is exacerbated because all of the parameters (k, n, and T_c) are integral to the right-hand side. However, preliminary studies indicated that values of n on the order of 2 generally gave a satisfactory fit so that (3) could be recast as

$$(4) \quad T = T_c + k^{1/n}t^{-1/n}, \quad T \geq T_c$$

which is linear when a value of n is specified. The T-intercept of (4) is precisely the UILT (T_c). Herein lies the usefulness of the model: short-term experiments in the lethal zone yielding (T, t) data may be used to estimate T_c by means of (4). Furthermore, this estimation is equivalent to extrapolation to zero mortification rate, for, by (3),

$$(5) \quad m(T) = \frac{1}{t} = k^{-1}(T - T_c)^n, \quad T \geq T_c.$$

In particular,

$$\lim_{T \to T_c} m(T) = 0.$$

Although (3) implies that mortification rate is not linear in T, (5) shows that $m(T)^{1/n}$ is, so that the process of extrapolation to zero mortification rate can be linearized easily.

An exhaustive statistical analysis of model (3) was undertaken, using a broad selection of data from the literature. The analysis and conclusions are described in detail in the next section. In summary, we found that, providing an appropriate value of n is assumed, model (3) represents the data about as well as model (1), and that model (3) also permits reasonably accurate predictions of the UILT based only on the data from the

TABLE 1. Comparison of observed upper incipient lethal temperatures (UILT) of selected fish species with those predicted by the model for $n = 2.7$ (KS, Knoxville fish tested in summer; TW, Toronto fish tested in winter; TS, Toronto fish tested in summer; PS, Put-in-Bay, tested in summer).

Species	Acclimation level (°C)	Observed UILT (°C)	Predicted UILT (°C)	Error (°C)	Reference
Rhinichthys atratulus	20 KS	29.50	29.70	0.20	Hart 1952
Rhinichthys atratulus	20 TW	29.30	30.18	0.88	Hart 1952
Semotilus atromaculatus	25 TW	30.30	30.56	0.26	Hart 1952
Semotilus atromaculatus	25 TS	31.50	31.44	−0.06	Hart 1952
Notropis atherinoides	25 TW	30.70	31.49	0.79	Hart 1952
Hybognathus notatus	20 TW	31.70	32.35	0.65	Hart 1952
Hybognathus notatus	25 PS	34.00	33.94	−0.06	Hart 1952
Ictalurus nebulosus	20 PS	32.70	32.47	−0.23	Hart 1952
Ictalurus nebulosus	25 PS	33.70	33.24	−0.46	Hart 1952
Perca flavescens	25 TW	29.70	30.10	0.40	Hart 1952
Perca flavescens	25 PS	32.30	32.07	−0.23	Hart 1952
Salvelinus fontinalis	11	24.40	24.42	0.02	J. A. Sholdice[a]
Salvelinus fontinalis	14	23.80	24.22	0.42	This study
(Replicate)	14	23.80	24.30	0.50	This study
Salvelinus fontinalis	24	25.30	25.53	0.23	Fry et al. 1946
Salvelinus fontinalis	20	25.30	25.20	−0.10	Fry et al. 1946
Salvelinus fontinalis	20	24.50	24.50	0	Fry et al. 1946

[a]The manuscript containing J. A. Sholdice's upper lethal temperature data for *Salvelinus fontinalis* is available in the archives of the Wilfrid Laurier University Library.

zone of resistance. Curve *b* in Fig. 1A shows the representation by model (3) of the typical data, using the value of n (2.7) we found best for that particular grouping of species. This value of n is also used in Fig. 1B to show the extrapolation of $m^{1/n}$ to zero in order to predict the UILT. In this instance the observed UILT is 25.3°C and our "prediction" based only on the data from the zone of resistance is 25.2°C.

Statistical Analysis

In this section we describe the statistical tests applied to assess the ability of model (3) to represent data from the zone of thermal resistance and to judge how effectively (4) could predict the UILT from these data.

Data Sets

The goodness of fit of the model was tested using data from the literature. Upper lethal temperatures for many species of fish have been published over the last 45 yr, and especially during the last decade because of the concern over the thermal pollution of waters. In many studies, however, experiments have been carried out only in the zone of resistance, data from the transitional band and the zone of tolerance being absent (Coutant 1972). To test the mathematical model it was necessary to have data sets including observations in the zone of resistance and determinations of UILT. An extensive search of the literature produced about 40 data sets involving fish subjected only to thermal stress (see Tables 1 and 2) and satisfying these criteria. Each set included at least four observations in the zone of resistance.

Procedures and Results

The data sets were grouped in various ways for purposes of fitting the (T, t) data from the zone of resistance to (4), using a wide selection of values for n. The fits were judged according to the accuracy with which the T-intercepts of the fitted lines "predicted" the corresponding observed UILTs. The best groupings were those presented in Tables 1 and 2. For *Oncorhynchus* spp. (Table 2) the 24 data sets fit best at $n = 1.8$. For the other 17 data sets (Table 1), the best fit was obtained at $n = 2.7$. Using only data from the zone of resistance the observed UILT could be "predicted" within 0.5° in about 80% of the cases, and within 1.0° in about 98%.

As illustrated by Fig. 1A, models (1) and (3) were equally good at representing the data from the zone of resistance. Estimated correlations (r) in fits of (2) and (4) were about equal, and almost always exceeded 0.9 in absolute value. Because the two models provide similar representations of the data, a strong point in favour of model (3) is its ability to relate observations from the zone of resistance to the location of the boundary of this zone, an ability that model (1) lacks.

We undertook a more elaborate validation of model (3). Because the standard error (SE) of the T-intercept of the fitted line (4) can be calculated for each data set, the quantity (6) is a Student's t variate:

$$(6)\quad \frac{T_c\ (\text{predicted}) - T_c\ (\text{actual})}{\text{SE}}.$$

It has $N - 2$ degrees of freedom where N is the number of (t, T) pairs in the data set. Identifying T_c (actual) with the observed UILT permits the calculation of the value of expression (6) for each data set; if model (3) is correct, these values constitute independent observations from appropriate Student t distributions. For each such observation, the value q of the corresponding cumulative distribution function can be determined. These values of q represent independent observations of the value of a uniform variate on (0, 1), again provided that the models are correct. For each of the two groupings of data sets the observed distribution of q was tested against the uniform distribution on (0, 1) using the Kolmogorov–Smirnov test (Lindgren et al. 1978). In neither case was any significant departure from the

TABLE 2. Comparison of observed upper incipient lethal temperatures (UILTs) of *Oncorhynchus* spp. (Brett 1952) with those predicted from the model $n = 1.8$.

Species	Acclimation level (°C)	Observed UILT (°C)	Predicted UILT (°C)	Error (°C)
O. tshawytscha	24	25.10	24.90	−0.20
O. tshawytscha	20	25.10	25.01	−0.09
O. tshawytscha	15	25.00	24.65	−0.35
O. tshawytscha	10	24.30	25.45	1.15
O. tshawytscha	5	21.50	21.19	−0.31
O. gorbuscha	20	23.90	24.47	0.57
O. gorbuscha	15	23.10	23.34	0.24
O. gorbuscha	10	22.50	22.52	0.02
O. gorbuscha	5	21.30	21.17	−0.13
O. gorbuscha	24	23.90	24.89	0.99
O. kisutch	23	25.00	24.84	−0.16
O. kisutch	20	25.00	25.24	0.24
O. kisutch	15	24.30	24.34	0.04
O. kisutch	10	23.70	23.99	0.29
O. keta	23	23.80	24.24	0.44
O. keta	20	23.70	24.05	0.35
O. keta	15	23.10	23.56	0.46
O. keta	10	22.60	22.39	−0.21
O. keta	10	21.80	21.46	−0.34
O. nerka	23	24.30	24.16	−0.14
O. nerka	20	24.80	24.68	−0.12
O. nerka	15	24.40	24.17	−0.23
O. nerka	10	23.40	23.11	−0.29
O. nerka	5	22.20	21.46	−0.74

hypothesized uniform distribution detected. For the grouping of Table 1, $D_{max} = 0.1249$ whereas $P(D_{max} > 0.250) = 0.20$, and for the grouping of Table 2, $D_{max} = 0.1727$ whereas $P(D_{max} > 0.216) = 0.20$. The Kolmogorov–Smirnov test thus indicates that both groupings of data sets are consistent with model (3) when appropriate values of n are chosen.

Notwithstanding the failure of the Kolmogorov–Smirnov test to detect significant deviations from model (3), there are several outliers within each grouping (see Tables 1 and 2). The Kolmogorov–Smirnov test is a nonparametric test known to be insensitive to deviations in the tails of the hypothesized distribution. Nevertheless, the agreement with the model is quite good considering that there are several sources of error not accounted for in the analysis. First, distributions of survival times have heavier tails than the normally distributed data assumed in the least squares fit of (4) and the calculations of SE in (6). Secondly, the replacement in (6) of T_c (actual) by the observed UILT injects an experimental error into the calculation. This experimental error is difficult to estimate and impossible to account for. Finally, it seems likely that the "true" value of n varies slowly across and perhaps within species. If data sets corresponding to different values of n are grouped together, the substitution of an approximate for an actual value for n constitutes another source of error of unknown magnitude. In summary, then, the agreement of the predicted UILTs based on model (3) with observed values is at least as good as could reasonably be expected, and certainly good enough to recommend (3) as an accurate and useful representation of the data.

A further point about the value of n concerns the nonlinear least squares method, which could be used to estimate all three parameters of equation (3) simultaneously. This undertaking could give a much clearer indication of how (and if) the value of n varies across species, acclimation temperatures, etc. It would be a good topic for a future study.

Prediction of UILTs

In general, model (3) represents data from the zone of resistance about as well as model (1) and provides the additional feature of predictions of the UILT. The value of n giving the best predictions for our first group of data sets (Table 1) was 2.7. Data (Table 2) for the genus *Oncorhynchus*, in contrast, fit best at $n = 1.8$. In both cases "predicted" UILTs agreed with observed usually to within 0.5° and almost always to within 1°. This is accuracy sufficient for useful predictions in many situations. The discrepancy between the best values of n for our first and second groups of data sets is of some interest. It reflects the different shape of the temperature–time curves for the primarily cool and warm-water species of Table 1 and the stenothermal group of Table 2.

Designing Lethal Temperature Experiments

Our new model is useful in the design and conduct of experiments to determine upper lethal temperatures of fish. Such tests usually last 1 wk and require regular and frequent observations. An approximation to the curve relating lethality and temperature would facilitate scheduling experiments to effect economies in use of fish and in human effort. The model we developed permits the prediction of UILTs from the results of acute (≤12 h) experiments. To determine the parameters of model (3) an initial test temperature is chosen so that the median time to death of a sample is approximately 1 h. Two additional test baths are then set at temperatures 0.5° and 1° lower and the median times to death of each of the samples calculated. From this information the fit of (4), using an appropriate value of n, gives a reasonable initial approximation to the UILT. For all species, $n = 2$ appears to give a good first approximation, and makes calculations easy.

Application of the Model to Bioassays of Acute Toxicity

Model (3) was originally developed to describe the pattern of mortality when high temperature is the lethal agent. There is an analogy between lethal temperature determinations and toxicity bioassays; it appears that model (3) may be applied to describe the relation between LT50s and the concentration of the toxicant. As with the thermal model a straight line fits the data quite well when a suitable value of n is chosen in (4). The intercept of this line provides an estimate of the LC50 corresponding to a long exposure time — typically 144 h.

Table 3 summarizes the analysis of representative data from Dixon (1980). This study contains not only the customary LC50s (144 h) but also data from which LT50s for various concentrations of toxicant can be calculated. Following the same procedure as used in fitting thermal data, we found that the best fits resulted from $n = 0.38$. Lines fitted using this value in (4) resulted in agreement between observed and "predicted" LC50s (144 h), which was comparable with that found in the thermal data. Applications of (3) to toxicity experiments are identical to those for the thermal experiments previously described. As above, predictions of the curve describing the pattern of mortality in bioassay experiments assist in their

TABLE 3. Comparison of observed and estimated LC50 (144 h) for young rainbow trout (*Salmo gairdneri*) exposed to copper ion and HCN. Data coded by Dixon (1980). $n = 0.38$.

Data set	LC50 (observed) (μg/L)	LC50 (estimated) (μg/L)	Error
CU-94-14-CU-C	324.0	318.6	−5.4
CU-94-0-CU-PE	316.0	299.6	−16.4
CU-94-7-CU-PE	450.0	427.3	−22.7
CU-94-14-CU-PE	472.0	500.3	28.3
CU-94-21-CU-PE	515.0	495.9	−19.1
CU-30-0-CU-C	294.0	272.0	−22.0
CU-30-7-CU-C	328.0	329.8	1.8
HCN-34-7-HCN-PE	67.0	84.5	17.5
CU-94-0-CU-C	328.0	420.3	92.3
CU-94-7-CU-C	304.0	453.4	149.4

design. There are many data sets in the literature that do not include tests of duration greater than 24 h. In the absence of data from long-term experiments, good approximations of the LC50 corresponding to these data sets may be obtained from this model.

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A Bioeconomic Analysis of Sequential Fisheries: Competition, Coexistence, and Optimal Harvest Allocation Between Inshore and Offshore Fleets

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A bioeconomic model is developed to determine optimal harvest allocation between "offshore" and "inshore" fleets exploiting a single fish stock in sequential fisheries. The socially optimal policy for maximizing total discounted rent is determined in terms of optimal escapement levels in each fishery. Whether exclusion or coexistence of the two fleets occurs under open access and under optimal management is found to depend primarily on inshore/offshore price and cost ratios, together with biological parameters related to the age structure of the fish stock. We discuss how fishery regulations, such as separate landings taxes imposed on each fleet, can be used to jointly optimize open-access exploitation in sequential fisheries.

Les auteurs ont élaboré un modèle bioéconomique pour déterminer la répartition optimale des contingents entre les secteurs côtier et hauturier qui exploitent un seul stock de poissons au cours de pêches consécutives. La politique sociale optimale permettant de maximiser la rente totale escomptée est déterminée en fonction des niveaux optimaux d'échappée dans chaque pêche. L'exclusion ou la coexistence des deux flottilles en vertu d'un accès libre et d'une gestion optimale dépend surtout des rapports coûts / avantages de la pêche côtière et hauturière et des paramètres biologiques de la structure des âges dans les stocks de poisson. Les auteurs examinent comment des règlements de pêche, comme l'imposition à chaque flottille de taxes au débarquement de montants distincts, peuvent être utilisés pour optimiser conjointement l'exploitation à accès libre de pêches consécutives.

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While the biological complexities of fisheries management have received considerable attention in the literature (for example, Clark 1976; Ludwig and Walters 1982; Mendelssohn 1978; Reed 1974), an equally important complicating aspect involves complexity in the structure of the fishery itself. In many fisheries, a single fish population is harvested sequentially by a series of separate, discrete fisheries. The pattern of such "gauntlet" fisheries can include (i) harvesting by different fleets at different stages in the life cycle of the fish stock, (ii) simultaneous or near simultaneous harvesting by different fleets, or (iii) sequential harvesting by the same fleet but at two separate times and possibly at different geographical locations. Typically, these fisheries involve conflicts between users of the fish resource, due to differences in types of fishing gear, location, or timing of fishing.

In cases such as these, management of each fishery in isolation ignores the fact that the fisheries are linked through their exploitation of the same fish stock, while aggregating the fisheries together ignores economic differences between them, as well as differences in the biological impact of each fishery on the fish stock. The optimal fleet mix and optimal catch allocation to each fishery must involve a balance between these economic and biological factors. A model to accomplish this is developed herein, to provide an analytical framework for examining optimal harvesting strategy, optimal catch allocation, and questions of exclusion or coexistence of the fisheries under optimal management and under open-access conditions.

In the model, it will be assumed, for simplicity, that precisely two fisheries are possible each season; the first (referred to here as the *offshore* fishery) is based on the entire fish stock, while the second (the *inshore* fishery) harvests only spawners. Note that if the entire vulnerable offshore population moves inshore to spawn each year, then both fisheries are in fact harvesting from the entire fish stock; an example of this special case will be discussed in the following section.

The model is applied to a study of economic and policy aspects concerning the allocation question. How do economic factors (unit prices and costs) determine the equilibrium configuration of the fishery: exclusion of one of the fisheries or coexistence of both? How does the open-access bionomic equilibrium compare with optimal harvest allocation? How can

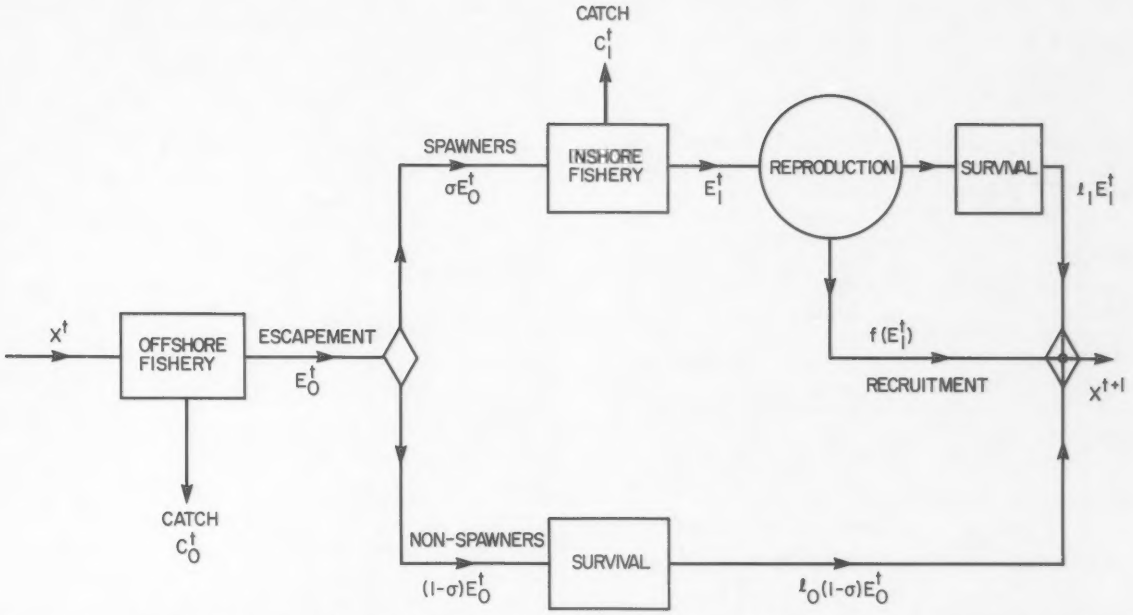

FIG. 1. General structure of a sequential fishery, as assumed in the model. Note that if $\sigma = 1$, implicit age structure is suppressed, and the model assumes two successive fisheries on the same fish stock.

regulatory tools be used to move the open-access fishery towards optimum?

The optimal management of sequential fisheries has received little attention to date, at least within the context of bioeconomic analysis. The related question of multiple fleets harvesting a single fish stock has received some attention, notably in the work of Clark and Kirkwood (1979) and McKelvey (1983). These papers examined problems of optimal fleet mix from the perspective of determining optimal capacities for each fleet. However, by assuming that the fleets harvest simultaneously, the structural aspects of sequential fisheries were not emphasized.

The Model

To motivate the derivation of a suitable model, we first discuss a simplified depiction of a particular gauntlet fishery, targetted on British Columbia chinook salmon (*Oncorhynchus tshawytscha*). Salmon trollers harvest both spawners (adults) and nonspawners (juveniles), while net boats (gill-netters and purse-seiners) tend to catch primarily spawning chinook. The average age and weight of a troll-caught salmon is typically less than that of a net-caught (spawning) fish, but since the former are considered to be of higher quality than those caught by inshore nets closer to the spawning grounds, the price *per fish* is assumed to be higher for chinook salmon caught by trollers. However, fishing costs per unit harvest will also be higher for trollers in general, since greater distances must be travelled to reach offshore fishing grounds. Finally, while a fish foregone by the troll fleet may contribute neither to the inshore net catch nor to the spawning effort (due to natural mortality), a fish that escapes from inshore nets has a relatively high probability of spawning and hence is of greater benefit to future chinook stock sizes. These factors combine to make management of such fisheries a particularly complex problem.

Consider now an aggregated fish stock whose size (in numbers of fish) at the beginning of the fishing season in year t is X^t. Suppose that the offshore fishery acts first on the stock and removes C_0^t fish, with a resulting escapement of E_0^t. Neglecting natural mortality during the offshore fishing season, we have $E_0^t = X^t - C_0^t$. Suppose that a fixed proportion σ of the escapement from the offshore fishery move inshore to spawn in each year, and that the inshore fishery acts only on this spawning group. If the inshore catch is denoted by C_1^t, then $E_1^t = \sigma E_0^t - C_1^t$ is the inshore escapement. (Unless otherwise indicated the superscript will refer to time and the subscripts 0 and 1 to offshore or inshore, respectively.) Suppose that this spawning stock of E_1^t fish results in a subsequent recruitment $f(E_1^t)$ to the stock in year $t + 1$. Assume further that a proportion ℓ_1 of the spawners in year t survive to be part of the stock in year $t + 1$, and that a proportion ℓ_0 of the nonspawners similarly survive. The dynamics of the model are then given by the equation

$$X^{t+1} = \ell_0(1 - \sigma)E_0^t + \ell_1 E_1^t + f(E_1^t) \quad (1)$$

where

$$E_0^t = X^t - C_0^t$$

and

$$E_1^t = \sigma E_0^t - C_1^t.$$

The assumed fishery structure is depicted in Fig. 1.

For convenience we will lump the terms involving surviving spawners and new recruits into a single term by letting

$$F(E_1^t) = \ell_1 E_1^t + f(E_1^t). \quad (2)$$

This function, F, then represents an overall spawner to future-stock relationship, and will be assumed to be concave and increasing (exhibiting "normal compensation"). Equation (1) can then be written:

(3) $X^{t+1} = \beta E_0^t + F(E_1^t)$

where $\beta = \ell_0(1 - \sigma)$. This is the basic dynamic equation, subject to the natural constraints $0 \leq E_0^t \leq X^t$ and $0 \leq E_1^t \leq \sigma E_0^t$. This model in its generality applies to many exploited fish stocks. Specific cases are discussed at the end of this section.

We now turn to the economic aspects of the model. Let p_0, p_1 denote the price per fish (landed or wholesale) for the offshore and inshore fisheries, respectively. We assume in general that $p_0 > p_1$. Suppose that for both fisheries the assumptions underlying the Schaefer production function hold (see Clark 1976, p. 235). In this case the cost of catching a fish in the offshore fishery when the target population is at level x is c_0/x. Similarly in the inshore fishery the corresponding marginal cost is c_1/x. The total costs of the two harvests in year t are thus c_0 log (X^t/E_0^t) and c_1 log $(\sigma E_0^t/E_1^t)$, obtained by integrating the marginal costs between initial and final stock sizes for each fishery. We shall assume that inshore fishing is cheaper per unit effort than offshore fishing, i.e. that $c_0 > c_1$.

The annual rent produced by the two fisheries is thus

(4) $$\pi^t = p_0(X^t - E_0^t) - c_0 \log (X^t/E_0^t) + p_1(\sigma E_0^t - E_1^t) - c_1 \log (\sigma E_0^t/E_1^t).$$

Some special cases of the model are of interest.

"Chinook Salmon" Model

Setting $\ell_1 = 0$ in the model is equivalent to assuming that all spawners die after spawning, a biological feature characteristic of all species of Pacific salmon. With $\sigma < 1$ the model assumes that fish reach spawning maturity at several different ages, as is the case with chinook salmon. The offshore and inshore fisheries in this case correspond to troll and net fleets, as discussed previously.

"Pink Salmon" Model

If $\ell_1 = 0$ and $\sigma = 1$ we have a model in which all fish spawn at the same age and die after spawning. This is the case for pink salmon (*Oncorhynchus gorbuscha*) in the Northeast Pacific, which invariably spawn at age 2. Again the two relevant fisheries are the troll fishery (offshore) and the net fishery (inshore). In a given fishing season, the troll fishery takes place first, with the net fishery then acting on the escapement from the troll fishery.

From the point of view of analysis the pink salmon model is considerably simpler than the general model, since with $\beta = 0$ in equation (3) we have $X_{t+1} = F(E_1^t)$. The chinook model, on the other hand, does not provide any real simplification.

"Herring" Model

In recent history, the British Columbia Pacific herring (*Clupea harengus pallasi*) fishery has consisted of three primary components. Currently, the first fishery each season serves the relatively small, nonlucrative "food and bait" market and is aimed primarily at mature fish, with a limited harvest of juvenile nonspawners. Later in the season, after mature stocks of herring have moved to their spawning grounds, a "roe fishery" takes place, in which the spawning stock is harvested for the Japanese herring roe market.

This latter fishery began in the early 1970s; before that time the primary component to the British Columbia herring fishery was a reduction fishery producing fish meal and fish oil. This type of fishery, which no longer exists in British Columbia but is common in many locations around the world, harvests from the entire population (spawners and juveniles alike) in a relatively nonselective manner.

Since individual herring require differing lengths of time to reach sexual maturity, but then are able to spawn for several successive years, our model can be used to address optimal management of a sequential herring fishery by setting $\ell_0 > 0$, $\ell_1 > 0$, and $0 < \sigma < 1$. However, since the "food and bait" fishery does not target equally on spawners and nonspawners, the model would require slight modification before it could be fully applied to this herring fishery.

Bionomic Equilibrium

In this section we consider the Gordon (1954) bionomic equilibrium, resulting from open access to both inshore and offshore fisheries.

For the offshore fishery, when the fish population is at level x, the marginal return (per extra fish caught) is

$$p_0 - c_0/x.$$

Thus there will be an offshore fishery only if the initial population level x exceeds c_0/p_0. If this is the case then in the open-access situation with no limitations on effort, the offshore fishery will harvest the stock down to c_0/p_0, the zero marginal rent level.

Similarly the inshore fishery will operate only if the initial target population level σE_0 exceeds c_1/p_1 where E_0 is the escapement from the offshore fishery, $E_0 = \min(x, c_0/p_0)$. In this case with open access the resulting escapement level will be c_1/p_1, the zero marginal rent level.

Thus the bionomic equilibrium escapement levels $\hat{E}_0$ and $\hat{E}_1$ and initial stock level $\hat{X}$ are given by the three equations

(5) $$\hat{E}_0 = \begin{cases} \hat{X} & \text{if } \hat{X} \leq c_0/p_0 \\ c_0/p_0 & \text{if } \hat{X} > c_0/p_0 \end{cases}$$

(6) $$\hat{E}_1 = \begin{cases} \sigma\hat{E}_0 & \text{if } \sigma\hat{E}_0 \leq c_1/p_1 \\ c_1/p_1 & \text{if } \sigma\hat{E}_0 > c_1/p_1 \end{cases}$$

(7) $$\hat{X} = \beta\hat{E}_0 + F(\hat{E}_1).$$

The variable $\hat{X}$ can be eliminated from (5) and (7) through the use of some mathematical manipulation to show that

$$\hat{X} = \beta\hat{E}_0 + F(E_1) > c_0/p_0 \quad \text{if and only if } (1 - \beta)^{-1}F(\hat{E}_1) > c_0/p_0.$$

This allows the replacement of (5), (6), and (7) with the two equations

(8) $$\hat{E}_0 = \begin{cases} (1 - \beta)^{-1}F(\hat{E}_1) & \text{if } (1 - \beta)^{-1}F(\hat{E}_1) \leq c_0/p_0 \\ c_0/p_0 & \text{if } (1 - \beta)^{-1}F(\hat{E}_1) > c_0/p_0 \end{cases}$$

(9) $$\hat{E}_1 = \begin{cases} \sigma\hat{E}_0 & \text{if } \sigma\hat{E}_0 \leq c_1/p_1 \\ c_1/p_1 & \text{if } \sigma\hat{E}_0 > c_1/p_1, \end{cases}$$

i.e. $\hat{E}_0 = \min\{(1 - \beta)^{-1}F(\hat{E}_1), c_0/p_0\}$ and $\hat{E}_1 = \min\{\sigma\hat{E}_0, c_1/p_1\}$.

The solution to this pair can be obtained graphically. Four cases arise depending on which of the four regions in the E_0–E_1 plane defined by the curves $E_0 = (1 - \beta)^{-1}F(E_1)$ and $E_1 = \sigma E_0$, the point $P \equiv (c_0/p_0, c_1/p_1)$ falls in (see Fig. 2).

Case 1

If the point $P \equiv (c_0/p_0, c_1/p_1)$ falls in region A, i.e. if c_1/p_1

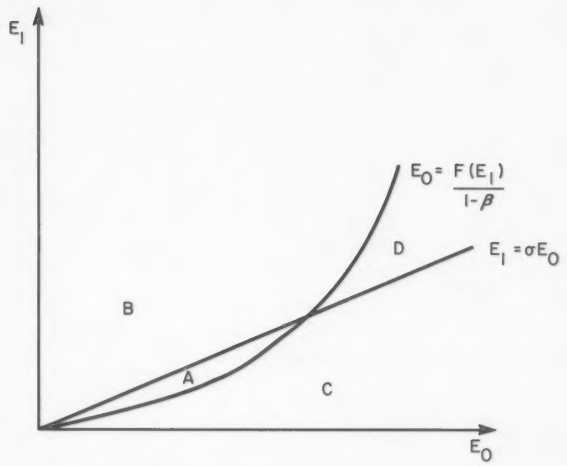

FIG. 2. The qualitative nature of the open-access bionomic equilibrium is determined by the location of the point $(c_0/p_0, c_1/p_1)$, representing offshore and inshore cost/price ratios, in relation to the four regions of the E_0–E_1 space.

$< \sigma c_0/p_0$ and $c_0/p_0 < (1-\beta)^{-1}F(c_1/p_1)$, then the graphs of equations (8) and (9) are given by the bold curves in Fig. 3a, and their solution is given by the point of intersection P. In this case in bionomic equilibrium both inshore and offshore fisheries coexist, with the offshore catch being $\beta c_0/p_0 + F(c_1/p_1) - c_0/p_0$ and the inshore catch being $\sigma c_0/p_0 - c_1/p_1$.

Case 2

If the point P falls in region B, then Fig. 3b applies, and the solution is at the point Q, where the bionomic equilibrium escapements are $\hat{E}_0 = c_0/p_0$ and $\hat{E}_1 = \sigma c_0/p_0$. In this case the inshore fishery is excluded in bionomic equilibrium.

Case 3

If the point P falls in region C, the solution lies at the point Q in Fig. 3c, so that the bionomic equilibrium escapements are $\hat{E}_1 = c_1/p_1$ and $\hat{E}_0 = (1-\beta)^{-1}F(c_1/p_1)$. In this case the offshore fishery is excluded in bionomic equilibrium.

Case 4

If the point P falls in region D, then the solution to (8) and (9) is given by the intersection, Q, of the bold curves in Fig. 3d. In this case, $\hat{E}_0$ is the solution to $\hat{E}_0 = (1-\beta)^{-1}F(\sigma\hat{E}_0)$, and $\hat{E}_1 = \sigma\hat{E}_0$, so that $\hat{E}_0$ is the unfished equilibrium stock level and $\hat{E}_1$ is the unfished equilibrium spawning level. In this case neither fishery can make a profit.

The results above can be summarized in terms of cost/price ratios. If there is open access to both fisheries then there will be an inshore fishery present in bionomic equilibrium if and only if $c_1/p_1 < \sigma c_0/p_0$, and there will be an offshore fishery present in bionomic equilibrium if and only if $c_0/p_0 < (1-\beta)^{-1}F(c_1/p_1)$. Coexistence of both fisheries in bionomic equilibrium will be possible if and only if

$$\frac{1}{\sigma}\left(\frac{c_1}{p_1}\right) < \left(\frac{c_0}{p_0}\right) < \frac{1}{1-\beta}F\left(\frac{c_1}{p_1}\right),$$

a condition that states that neither cost/price ratio can be too high with respect to the other.

Dynamic Optimization

In this section the optimal policy to maximize the discounted stream of rents from the resource will be analyzed in a dynamic setting.

It will be assumed that fishery rents π^t earned in year t will be discounted by a factor[1] α^t to a "year-zero" or present value $\alpha^t\pi^t$. The discount factor α is related to the annual discount rate, i, by $\alpha = 1/(1+i)$.

For a given exploitation pattern characterized by the sequence of escapements $\{(E_0^t, E_1^t)\}_{t=0}^{\infty}$, the present value of the stream of rents is

$$(10)\quad J = \sum_{t=0}^{\infty} \alpha^t\pi^t$$

where π^t is given by (4). The overall social objective will be assumed to be the maximization of the present value J over the sequence $\{(E_0^t, E_1^t)\}_{t=0}^{\infty}$ subject to the constraints

$$(11)\quad 0 \leq E_0^t \leq X^t$$

$$(12)\quad 0 \leq E_1^t \leq \sigma E_0^t$$

and the dynamic equation

$$(13)\quad X^{t+1} = \beta E_0^t + F(E_1^t).$$

This is a control problem involving a single state variable (X^t) and two control variables (E_0^t and E_1^t). The solution will be studied by means of the Discrete Maximum Principle (e.g. see Cannon et al. 1970).

To apply the Discrete Maximum Principle we define a Hamiltonian H^t:

$$(14)\quad H^t = \alpha^t\pi^t + \lambda^t(X^{t+1} - X^t)$$

where π^t is given by (4) and λ^t is the adjoint or co-state variable, representing the shadow value of the fish stock. Writing out the Hamiltonian in full, we obtain

$$(15)\quad H^t = \alpha^t[p_0(X^t - E_0^t) + p_1(\sigma E_0^t - E_1^t) + c_0 \log (E_0^t/X^t) + c_1 \log (E_1^t/\sigma E_0^t)] + \lambda^t[\beta E_0^t + F(E_1^t) - X^t].$$

In simple applications of the Discrete Maximum Principle, this Hamiltonian would be maximized over the control variables, and the resulting optimality equations combined with the adjoint equation for λ, to produce the overall solution. In this case the analysis is not as straightforward, due to the complexities involved in dealing with two controls and one state variable. The Hamiltonian must be considered as a function of the state X, treating the controls E_0 and E_1 as parameters temporarily. If $X > E_0$, equation (15) holds without modification. However, if instead we have $X \leq E_0$, which allows both for the case of no offshore fishery ($X = E_0$) and for mathematical continuity in the state variable X to levels less than E_0, then one must rewrite the Hamiltonian, replacing E_0^t by X^t throughout. In other words:

$$(16)\quad H^t = \alpha^t[p_1(\sigma X^t - E_1^t) + c_1 \log (E_1^t/\sigma X^t)] + \lambda^t[(\beta - 1)X^t + F(E_1^t)] \quad \text{if } X^t \leq E_0^t.$$

This essentially states that, for a fixed target offshore escapement E_0^t, if $X^t \leq E_0^t$, then there will be no offshore fishery and hence no offshore revenues or costs.

The Hamiltonian must be considered, therefore, as being piecewise defined by (15) and (16). Proceeding now with the

[1]In all of the following, α^t represents α raised to the tth power.

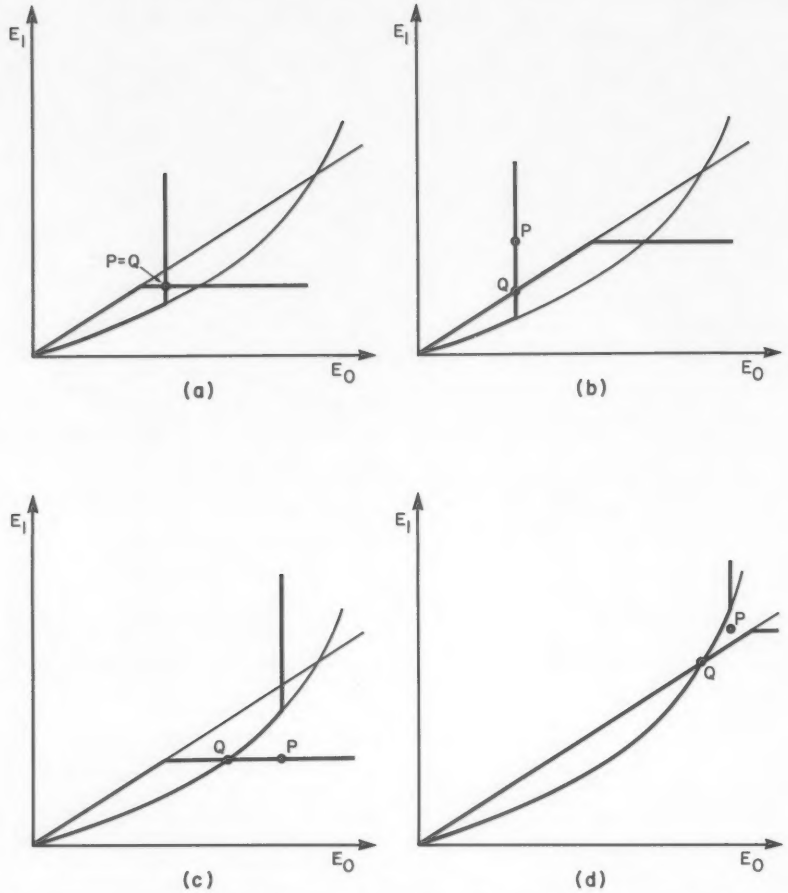

FIG. 3. Coexistence and exclusion in bionomic equilibrium. The point $(c_0/p_0, c_1/p_1)$ in E_0–E_1 space is represented by P. The bionomic equilibrium escapement pair $(\hat{E}_0, \hat{E}_1)$ is represented by Q, the intersection of the bold lines. (a) Coexistence of the two fleets; (b) exclusion of the inshore fishery; (c) exclusion of the offshore fishery; (d) the case in which neither fishery can make a profit, so that both are excluded.

derivation of the adjoint equation, we have

$$\lambda^t - \lambda^{t-1} = -\frac{\partial H^t}{\partial X^t} = \begin{cases} -\alpha^t(p_0 - c_0/X^t) + \lambda^t & \text{if } X^t > E_0^t \\ -\alpha^t(\sigma p_1 - c_1/X^t) + (1-\beta)\lambda^t & \text{if } X^t \leq E_0^t. \end{cases}$$

This can be simplified to the following:

$$\lambda^t = \begin{cases} \alpha^{t+1}(p_0 - c_0/X^{t+1}) & \text{if } X^{t+1} > E_0^{t+1} \\ \alpha^{t+1}\sigma(p_1 - c_1/\sigma X^{t+1}) + \beta\lambda^{t+1} & \text{if } X^{t+1} \leq E_0^{t+1}. \end{cases} \quad (17)$$

Equation (17) has a straightforward but interesting interpretation. If next year's fish stock, X^{t+1}, is sufficiently large so that an offshore fishery will be desirable ($X^{t+1} > E_0^{t+1}$), then the marginal shadow value of a nonexploited fish this year, λ^t, is equal to the marginal net benefits that will accrue next year, $p_0 - c_0/X^{t+1}$, discounted to year zero. On the other hand, if no offshore fishery will occur next year ($X^{t+1} \leq E_0^{t+1}$), then the shadow value of the resource is given by the sum of two components: (a) the discounted marginal net benefits of the spawning fraction of the fish stock, in next season's inshore fishery, and (b) the shadow value of the nonspawning portion of next year's fish stock that survives to the following year.

In theory, equations (15), (16), and (17) can be analyzed to obtain the optimal dynamic solution. However, the piecewise definition of the Hamiltonian and the adjoint variable greatly complicates the analysis, which will not be undertaken further in this paper. Instead, we turn now to the question of optimal equilibrium allocation, which can be analyzed in a more complete manner.

Optimal Equilibrium

In this section, equations are derived for the optimal stock and escapement levels in equilibrium. These can be related to the bionomic equilibrium under open access, in order to determine regulatory schemes that will produce a socially optimal pattern of exploitation in both the inshore and offshore fisheries under open-access conditions.

Let X, E_0, and E_1 now represent steady-state stock levels

satisfying $X = \beta E_0 + F(E_1)$. Inserting these quantities in the expressions for the Hamiltonian H^t and the adjoint variable λ^t, we have

$$(18)\quad H^t = \begin{cases} \alpha^t(-p_0E_0 + c_0 \log E_0 + \sigma p_1 E_0 - c_1 \log E_0) \\ \quad + \beta\lambda^t E_0 + \alpha^t(-p_1E_1 + c_1 \log E_1) \\ \quad + \lambda^t F(E_1) + \alpha^t(p_0X - c_0 \log X) - \lambda^t X \\ \qquad\qquad\qquad\qquad \text{if } X > E_0 \\ \alpha^t(\sigma p_1 X - p_1E_1 - c_1 \log(\sigma X) + c_1 \log E_1) \\ \quad + \lambda^t\beta X + \lambda^t F(E_1) - \lambda^t X \quad \text{if } X \leq E_0 \end{cases}$$

$$(19)\quad \lambda^t = \begin{cases} \alpha^{t+1}(p_0 - c_0/X) & \text{if } X > E_0 \\ \alpha^{t+1}\sigma(p_1 - c_1/\sigma X) + \beta\lambda^{t+1} & \text{if } X \leq E_0. \end{cases}$$

It is necessary to analyse the three possible outcomes (inshore fishery only, offshore fishery only, and coexistence) separately, to allow for the piecewise definition of H and λ.

Coexistence

If coexistence is optimal, we must have $X > E_0$ (for an offshore fishery to occur) so that the adjoint variable λ^t is specified from (19). However, it is also true in such a case that $\partial H/\partial E_1 = 0$, so that

$$\lambda^t = \alpha^t \frac{p_1 - c_1/E_1}{F'(E_1)}.$$

Combining the two expressions for λ^t, we obtain

$$(20)\quad p_1 - \frac{c_1}{E_1} = \alpha F'(E_1)\cdot\left(p_0 - \frac{c_0}{X}\right)$$

where $X = \beta E_0 + F(E_1)$. One must now consider in addition the decision variable E_0; setting $\partial H/\partial E_0 = 0$ produces

$$(21)\quad p_0 - \frac{c_0}{E_0} = \sigma\left(p_1 - \frac{c_1}{\sigma E_0}\right) + \alpha\beta\left(p_0 - \frac{c_0}{X}\right).$$

With $X = \beta E_0 + F(E_1)$, equations (20) and (21) can be solved simultaneously for both optimal escapement levels. These equations can be interpreted as follows. Given an offshore escapement E_0, equation (20) states that the optimal inshore escapement E_1 should be such that immediate marginal benefits $p_1 = c_1/E_1$ are balanced by the discounted future marginal rents that are foregone. Equation (21) sets the offshore escapement, given E_1, at a level such that immediate return from an additional unit harvest is equated to the sum of (a) the resulting foregone benefit to this season's inshore fishery and (b) the discounted marginal loss to next year's offshore fishery (due to harvest of nonspawners this season). Note that equations (20) and (21) can be written, respectively, as

$$E_1 = \phi_1(E_0)$$

and

$$E_0 = \phi_0(E_1)$$

where the function ϕ_1 is defined by equating the $(p_0 - c_0/X)$ terms in (20) and (21) to obtain

$$(20')\quad \frac{p_1 - c_1/E_1}{F'(E_1)} = \frac{1}{\beta}\left[(p_0 - \sigma p_1) - \frac{c_0 - c_1}{E_0}\right]$$

while $E_0 = \phi(E_1)$ can be formulated from (21) simply as the positive solution of the quadratic equation

$$(21')\quad E_0^2 + BE_0 + C = 0$$

where B and C are linear functions of $F(E_1)$.

Straightforward mathematical analysis shows that the functions ϕ_1 and ϕ_0 can be portrayed qualitatively as in Fig. 4a, with the optimal equilibrium given by the intersection point p.

Also shown in Fig. 4a are the constraint curves $E_1 = \sigma E_0$ and $E_0 = (1 - \beta)^{-1}F(E_1)$. As fishery characteristics vary, the coexisting equilibrium solution given by the simultaneous solution of (20) and (21) approaches one of these constraints in a smooth manner. In other words, it can be shown that the following single-fishery optimality equations (offshore only, inshore only) are identical (modulo some simple algebra) to the coexisting solution subject to the additional constraint $E_1 = \sigma E_0$ or $E_0 = X$, respectively. If the intersection of the two optimality equations lies outside region A of Fig. 2, exclusion of one or both fisheries must be optimal.

Offshore Only

In this case, $X = \beta E_0 + F(\sigma E_0) > E_0$, since $E_1 = \sigma E_0$ and the inequality $X > E_0$ is necessary for an offshore fishery to occur. Hence, λ^t is given by (19) with $X > E_0$, while

$$\frac{\partial H}{\partial E_0} = \alpha^t\left(-p_0 + \frac{c_0}{E_0}\right) + \beta\lambda^t + \lambda^t\sigma F'(\sigma E_0) = 0$$

must hold for an interior optimum. Combining these expressions, we obtain the optimality equation for offshore escapement E_0:

$$(22)\quad p_0 - \frac{c_0}{E_0} = \alpha[\beta + \sigma F'(\sigma E_0)]\left(p_0 - \frac{c_0}{X}\right).$$

The left-hand side of this equation is the marginal benefit obtainable from an additional unit harvest in the current season. The right-hand side is the marginal opportunity cost of that additional catch, in terms of foregone future harvest. It is the product of two terms: $\alpha(p_0 - c_0/X)$ is the discounted marginal value of an extra unit of the resource in the next season, while $\beta + \sigma F'(\sigma E_0)$ is a multiplier used to convert one offshore fish in the current year into the correct number of fish next year. This multiplier, in turn, is composed of two terms: survival of nonspawners plus incremental recruitment of "new" fish. Note that (22) can be rewritten in the standard Modified Golden Rule (MGR) form:

$$(23)\quad [\beta + \sigma F'(\sigma E_0)]\frac{p_0 - c_0/X}{p_0 - c_0/E_0} = \frac{1}{\alpha}.$$

In this form, it is evident that if $\beta = 0$ (no resident nonspawning stock offshore), then this "offshore only" result reduces to the standard single-stock, single-fishery solution (Clark 1976).

Figure 4b shows the situation diagrammatically. The optimality curves $E_1 = \phi(E_0)$ and $E_0 = \phi_0(E_1)$ intersect outside the constraint set and above the line $E_1 = \sigma E_0$. The desired equilibrium (E_0^*, σE_0^*), with E_0^* given by (22) or (23), will then lie on the line $E_1 = \sigma E_0$ at some point Q.

Inshore Only

In this case, $E_0 = X$ so $X = \beta X + F(E_1)$ and we thus have $X = (1 - \beta)^{-1}F(E_1)$. The adjoint variable is then given by (19) with $X \leq E_0$. An additional relationship can be obtained by

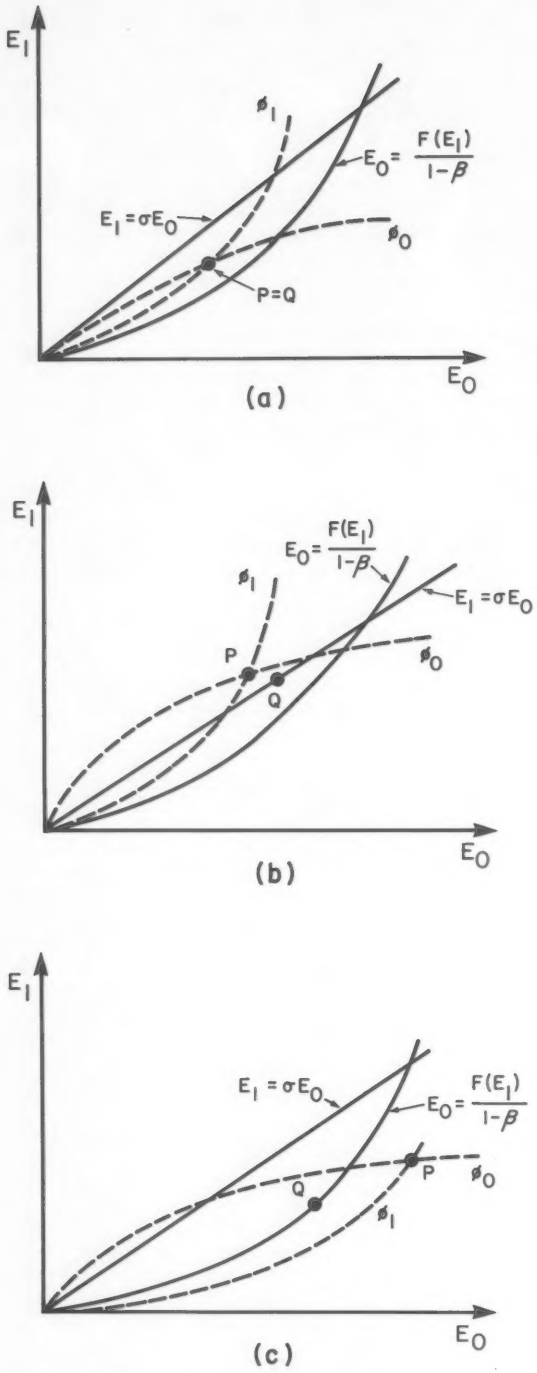

FIG. 4. Optimality curves $E_1 = \phi_1(E_0)$ and $E_0 = \phi_0(E_1)$ depicted (broken lines) together with the constraint curves $E_1 = \sigma E_0$ and $E_0 = F(E_1)/(1 - \beta)$. The location of the intersection point P of the optimality curves in relation to the constraints determines the nature of the optimal equilibrium. (a) Coexistence; (b) exclusion of the inshore fishery; (c) exclusion of the offshore fishery. Point Q represents the approximate location of the actual optimal equilibrium.

maximizing the Hamiltonian over inshore escapements E_1:

$$\frac{\partial H}{\partial E_1} = \alpha^t\left(-p_1 + \frac{c_1}{E_1}\right) + \lambda F'(E_1) = 0,$$

which can be rewritten

$$(24) \quad \lambda^t = \alpha^t \frac{p_1 - c_1/E_1}{F'(E_1)}.$$

Combining (24) with (19) and simplifying produces the optimality equation:

$$(25) \quad p_1 - \frac{c_1}{E_1} = \alpha\sigma F'(E_1)\left(p - \frac{c_1}{\sigma X}\right) + \alpha\beta\left(p_1 - \frac{c_1}{E_1}\right).$$

The left-hand side represents the immediate benefit of an incremental harvest in the inshore fishery. The right-hand side is the total foregone rents if that incremental catch is taken in the current season. This is composed of (a) the discounted loss to next year's inshore fishery and (b) the future loss due to foregone survival of offshore fish beyond the next season. Note that the term $(p_1 - c_1/E_1)$ appears on the right-hand side of (25), representing the current value of an additional unit of fish in the sea *next year*. Equation (25) can be written in a more standard MGR form:

$$(26) \quad \sigma F'(E_1)\frac{p_1 - c_1/\sigma X}{p - c_1/E_1} = \frac{1}{\alpha} - \beta = 1 + i - \beta$$

where i is the discount rate, $i = (1 - \alpha)/\alpha$.

Apart from the parameters β and σ, this represents the usual single-species optimality result. However, the role of nonspawning offshore fish becomes apparent from this formulation. The lower the fraction (σ) of offshore fish that spawn each year, the greater is the parameter β, since $\beta = \ell_0(1 - \sigma)$. In determining the optimal inshore escapement level, the offshore nonspawning stock plays the role of a "reserve," acting as a "bank account," on which the fishery draws each year to sustain

TABLE 1. Optimal equilibrium configuration (X, E_0^*, E_1^*) for each pair (p_1/p_0, c_1/c_0) of price and cost ratios. Also shown is an indication of whether the equilibrium of the fishery involves only "inshore" fishing, only "offshore," or "coexistence." See text for details.

Price ratio p_1/p_0	Cost ratio c_1/c_0 0.1	0.3	0.5	0.7
1.0	4.08 4.08 1.60 Inshore	4.58 4.58 1.94 Inshore	4.88 4.38 2.23 Coexist	4.92 3.02 2.42 Offshore
0.9	4.56 4.56 1.93 Inshore	4.81 3.60 2.25 Coexist	4.92 3.02 2.42 Offshore	
0.8	4.82 3.28 2.29 Coexist	4.92 3.02 2.42 Offshore		
0.7	4.92 3.02 2.42 Offshore			

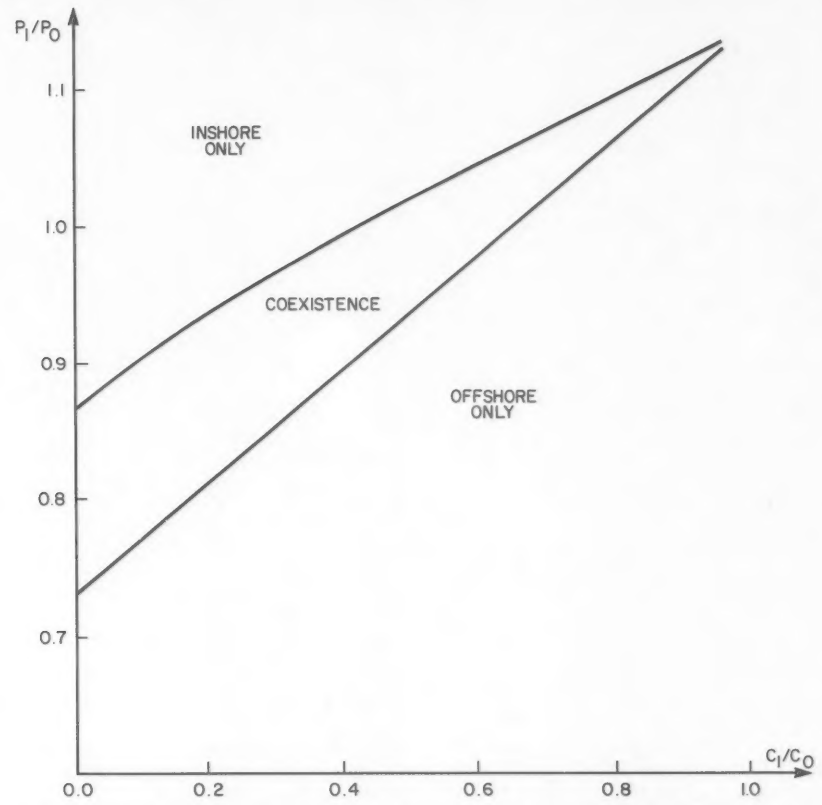

FIG. 5. Nature of the optimal equilibrium as a function of the price ratio p_1/p_0 and the cost ratio c_1/c_0. Model parameters used to obtain these results are described in the text.

the inshore stock. With this analogy, the result of equation (26) seems reasonable: the larger is β, the greater is the effect of the offshore "fish bank," and the lower is the effective discount rate $i - \beta$. It should be noted that β also enters equation (26) through the term $X = (1 - \beta)^{-1}F(E_1)$, but the effect is still to make management more conservationist.

The "inshore only" result is shown diagrammatically in Fig. 4c, where the coexistence optimality curves ϕ_0 and ϕ_1 intersect below the constraint $E_0 = (1 - \beta)^{-1}F(E_1)$. Hence, the optimal escapements $((1 - \beta)^{-1}F(E_1^*), E_1^*)$ given by (26) lie on this constraint curve, at some point Q.

The Role of Biological and Economic Parameters

From both the dynamic analysis and the equilibrium results, clearly price and cost differentials are major factors in determining the optimal balance between inshore and offshore fisheries. Indeed the common situation in which higher prices for fish caught offshore compete with lower inshore fishing costs leads to ongoing debates between gear types. To examine these price and cost questions in more detail, we turn now to a numerical analysis of equilibrium stock and escapement levels when the economic parameters are varied. Specifically, for fixed offshore parameters p_0 and c_0, the price ratio p_1/p_0 and the cost ratio c_1/c_0 have been varied, and the values of the optimal equilibrium biomass $\hat{X}$ and escapements $\hat{E}_0^*$ and $\hat{E}_1^*$ were determined for each parameter combination. Table 1 shows a set of typical results based on a Beverton–Holt stock–recruitment function

$$F(S) = \ell_1 S + \frac{aS}{b + S}$$

with the following arbitrarily chosen parameter values: $p = 1.0$, $c_0 = 1.0 \times 10^6$, $\alpha = 0.9$, $\ell_0 = 0.6$, $\ell_1 = 0.3$, $\sigma = 0.8$, $a = 7 \times 10^6$, and $b = 2 \times 10^6$. For each pair $(p_1/p_0, c_1/c_0)$ a triplet of numbers $(\hat{X}, \hat{E}_0^*, \hat{E}_1^*)$ is given, along with an indication of the optimal fleet composition. These results are displayed graphically in Fig. 5, which shows regions of coexistence and of exclusion. Similar results were obtained for other economic parameter values. Note that if the inshore fishery is excluded the equilibrium levels $(\hat{X}, \hat{E}_0^*, \hat{E}_1^*)$ are independent of the inshore parameters p_1 and c_1.

As expected, the inshore fishery dominates when p_1/p_0 is relatively high and c_1/c_0 is low, while operation of the offshore fishery alone is optimal when the reverse is true.

Particularly interesting is the intermediate region of coexistence between the inshore and offshore fisheries. If inshore fishing costs are very low, coexistence is optimal for a fairly substantial range of the inshore/offshore price ratio. If the inshore unit cost c_1 is closer to the offshore cost c_0, coexistence is constrained to an increasingly narrow range of the price ratio p_1/p_0. Figure 5 shows this result for cost ratios in the range $0 \leq c_1/c_0 \leq 0.95$.

Note that for the set of parameter values used here, when the cost ratio c_1/c_0 is large (inshore costs comparable with offshore

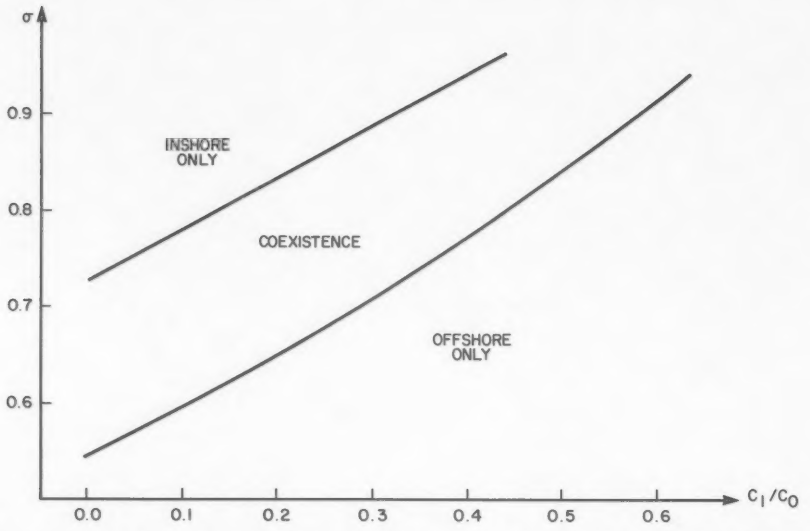

FIG. 6. Nature of the optimal equilibrium as a function of the spawning fraction σ and the inshore/offshore cost ratio c_1/c_0 (with p_1/p_0 fixed at 0.9). Regions of coexistence and exclusion depend in addition on other model parameters, which are described in the text.

costs), coexistence is optimal only when the inshore price actually exceeds the offshore price. Conversely, if $p_0 = p_1$, *exclusion* of the inshore fishery is optimal whenever $c_1/c_0 > 0.65$. The reason for this is that the greater availability of fish offshore can, up to a point, more than compensate for higher fishing costs. Of course, quantitative results will depend on the actual values of the biological parameters β and σ, but qualitative results seem robust to the choice of parameters.

Note also that in Table 1 the equilibrium fish stock $\hat{X}$ and the equilibrium spawning escapement $\hat{E}_1^*$ both decrease as the inshore fishery becomes more profitable. When high values of the price ratio p_1/p_0 combine with low values of the cost ratio c_1/c_0, the inshore fleet predominates, and harvests at a rate high enough to reduce both $\hat{X}$ and $\hat{E}_1^*$. With a low price ratio or a high cost ratio, the offshore fleet is dominant.

The biological parameter σ, representing the fraction of the total offshore fish population that moves inshore to spawn in any given year, appears to play a key role in determining the optimal equilibrium configuration in a sequential fishery. This parameter is a measure of the age structure occurring in the "vulnerable" fish population. In the case of pink salmon, all vulnerable fish in the offshore pool move inshore to spawn, so that $\sigma = 1$. Chinook salmon and herring, on the other hand, are harvested by the offshore fleet as both mature and immature fish, and hence a fraction of the offshore pool does not spawn ($\sigma < 1$).

Figure 6 shows the role of σ in determining the outcome (coexistence or exclusion) in the optimal equilibrium configuration. Although all fishery parameters interact to affect this outcome, the inshore unit cost c_1 has been used here as an indicator of the relative profitability of the inshore and offshore fisheries (holding p_1, p_0, and c_0 constant). Figure 6 depicts, then, the interaction between the biological parameter σ and the economic parameter c_1, with other parameters fixed as above.

One can see that the relative advantage of the inshore fishery increases as σ rises. When σ is small, the inshore fishery should be excluded, while at high values of σ the offshore fleet should not operate (unless inshore costs are high). There is a critical value of σ (in this case $\sigma_c = 0.54$) below which the inshore fleet is excluded even if its operating costs are negligible. Likewise there is a value of c_1 above which inshore costs are prohibitive even if all offshore fish spawn each year ($\sigma \cong 1$), and again only the offshore fishery should take place. As in Fig. 5, a band of (c_1, σ) combinations exists for which coexistence of the two fleets is optimal.

These results reflect the basic structure of the sequential fishery. When σ is small, inshore costs per unit harvest are relatively high, simply because fewer fish move inshore (i.e. c_1/x is large if x is small). Therefore there is little incentive to have an inshore fishery. Even if σ is large, however, the marginal offshore profit from a unit harvest, $p_0 - c_0/x$, may exceed the inshore equivalent, $p_1 - c_1/x$, if the parameter c_1 is large; in such cases the inshore fleet will again be excluded. It should be noted that this interaction also depends on the relative magnitudes of the inshore and offshore survival rates, ℓ_1 and ℓ_0, but these complications will not be addressed here.

To summarize the role of economic and biological parameters, an examination of the price and costs ratios, p_1/p_0, and c_1/c_0, together with the spawning fraction σ, appears sufficient to analyze the tradeoff involved in optimizing a sequential fishery.

Fishery Regulation

We have shown that optimal management of a structured sequential fishery can be achieved through controlling the escapement of fish from each fishery along the "gauntlet." Implicitly, this involves managing both the final spawning escapement and the allocation of available harvest between participating fleets. Traditionally, these two management aims have been treated separately, the former as "biological management" and the latter as a form of "political management" designed to maintain some equitable level of satisfaction (or dissatisfaction) amongst the relevant user groups. Our results show that this separation is not valid for sequential fisheries in

which competing fleets have differing prices, costs, and impacts on the fish stock. In such situations, determinations of optimal spawner levels and optimal catch allocations are tied together; arbitrary changes in catch allocation will typically produce suboptimal utilization of the resource.

A number of regulatory strategies exist for achieving optimal management of a sequential fishery. In-season catch monitoring can be used together with fishery closures, in order to achieve escapement goals in each fishery. This approach involves direct regulation and information requirements that can be expensive, but has the advantage of permitting the in-season incorporation of new information about stock size. The setting of fleet-specific catch quotas may be a promising method for simultaneously achieving overall catch level and the desired allocation of this catch. This regulatory method is particularly suited to management of a stable equilibrium fish stock; the presence of extensive year-to-year fluctuations would necessitate in-season updating of stock size estimates and hence of appropriate catch quotas.

A further option for fishery management may be the setting of separate landings taxes on each of the sequential fisheries. We consider this indirect form of economic regulation in somewhat more detail, since it fits well within the framework of this paper, although as with other regulatory measures, taxes must reflect annual fluctuations together with other uncertainties, and hence are by no means a simple solution.

An optimal taxation scheme changes the effective cost/price ratios to enable a socially optimal exploitation pattern to be realized through open access. Suppose taxes are imposed at the rates of t_0 dollars per fish landed offshore and t_1 dollars per fish landed inshore. Then the effective prices to the fishermen become $p_0 - t_0$ and $p_1 - t_1$, respectively. We wish to choose values of t_0 and t_1 to make the bionomic equilibrium derived earlier coincide with the socially optimal equilibrium. By examining separately the three cases involving coexistence or exclusion, corresponding to Fig. 4a, 4b, and 4c, specific taxation results can be obtained for each possible pattern of exploitation. Graphically the objective is to make the equilibrium point Q in Fig. 3 coincide with its optimal counterpart in Fig. 4.

An examination of these figures shows that, given the actual optimum escapements $\hat{E}_0^*$ and $\hat{E}_1^*$ together with the corresponding fleet configuration, sufficient taxes to optimize the equilibrium open-access fishery are $t_0 = p_0 - c_0/\hat{E}_0^*$ and $t_1 = p_1 - c_1/\hat{E}_1^*$. Although these are not necessarily the optimal *dynamic* taxes (see Clark 1976, p. 116), they do hold in equilibrium and they are sufficient to drive an unregulated open-access fishery to the optimum.

Discussion

We have provided an analytical framework for examining optimal fleet and catch allocation between the inshore and offshore components in sequential "gauntlet" fisheries. The model we analyzed is based on the assumption that the offshore fishery harvests from the whole fish population, while the inshore fishery exploits only fish that are heading towards their spawning grounds. This is the case, for example, in many salmon and herring fisheries. Although we have referred to "inshore" and "offshore" fisheries, it was pointed out that the *timing* of the sequential fisheries is of importance, not the geographical location; indeed, the fisheries may occur in precisely the same location. Age structure is implicitly included in the model, and indeed is a fundamental feature, since adult spawners and nonspawning juveniles play very different roles. By a judicious choice of the biological parameters, the model can also deal with two fisheries that act sequentially on the same mature fish stock, but that use different types of gear. However, this involves the loss of the age-structure component of the model, and hence is useful only for such cases as the British Columbia pink salmon fishery, where juvenile fish are not generally relevant to the fishery.

Economic factors have been summarized in the form of price and fishing cost parameters. While ignoring possible price elasticity and nonlinear costs, the model is sufficient to show the fundamental economic tradeoffs which determine optimal fleet allocation. In particular, the two cost/price ratios c_0/p_0 and c_1/p_1 determined the open-access bionomic equilibrium. Numerical results involving only variation of the price ratio p_1/p_0 and the cost ratio c_1/c_0 were adequate to illustrate the three possible optimal equilibrium fleet allocation scenarios: exclusion of the inshore fleet, coexistence of the inshore and offshore fisheries, and exclusion of the offshore fleet. On the other hand, analytic results showed that the full socially optimal solution depends in a more complicated manner on the prices and costs.

The social optimum is also strongly influenced by biological parameters, in particular the fraction of the offshore stock that spawns each season (σ). When σ is small, there should be no inshore fishery, while if σ is large an inshore fishery may be desired, and indeed the offshore fishery may be excluded in equilibrium.

The possible optimality of coexistence between inshore and offshore fishing fleets has been emphasized in this paper. Numerically, coexistence will occur only for a fairly narrow range of price and cost parameters. Furthermore, from our results it appears that coexistence will arise in the optimal solution only if the spawning fraction σ is sufficiently large; analytic results proved this to be the case also for the open-access equilibrium.

Analysis of coexistence versus exclusion under optimal exploitation can depend substantially on whether the dynamic or the equilibrium solution is being considered. Even if the optimal equilibrium configuration involves only the inshore fishery, a full dynamic solution may show that the offshore fleet is still desired in years of high fish stock abundance. For example, variable offshore costs per unit harvest may be sufficiently low to warrant the operation of an offshore fishery, which would then be phased out as stocks decline to equilibrium. In such cases, the offshore fishery would absorb catch variability, while the inshore catch remains relatively stable. In fact, in some situations an exceptionally good year may make it desirable to bring a previously excluded offshore fleet back into the fishery. However, such dynamic aspects of inshore/offshore allocation are complicated if fleet capital is nonmalleable (Charles 1983a; Clark et al. 1979), so that fishing boats have no alternative uses outside the fishery. In such cases, if these vessels are restricted from operating in the fishery, opportunity costs of this idle capital and physical depreciation of the vessels may make the decision to exclude one gear type from the fishery essentially irreversible. Furthermore, in the absence of an offshore fleet, the possible optimality of introducing such a fleet for a temporary period of "mining" an abundant resource will depend on a full analysis of joint fleet investment and harvest management. With stochastic resource fluctuations, this becomes a complex problem of investment under uncertainty (Charles 1983b). The extent of capital malleability will determine to a large degree whether the fleet mix will respond to such stochastic effects over time or whether the equilibrium configuration, once attained, will predominate in the fishery.

Finally, we discussed various regulatory methods for managing sequential fisheries. We found that taxes can be used to adjust the open-access equilibrium fishery to match the social optimum. Two distinct taxes are required on the inshore and offshore catches separately; in equilibrium, these optimal taxes are determined in terms of E_0^* and E_1^*, the optimal equilibrium escapement levels. Such taxes (or other regulatory measures) could be applied, for example, in the British Columbia herring fishery, where the "offshore" food fishery is not desired from the point of view of economic efficiency, but in fact exists primarily because it is the first fishery available each season. To maximize *total* rents, this fishery perhaps should be foregone entirely, but the optimal decision for many individual fishermen is to take part in both the offshore and inshore fisheries. Appropriate fishery regulation may serve as a tool to transform this coexisting fishery into an inshore-only fishery.

Of course, considerations other than simple rent maximization can play an important role in determining allocations between fisheries. In some cases, the offshore and inshore fisheries may appeal to completely separate markets, so that by maintaining both fisheries, at least to a limited extent, fisheries management can achieve a measure of demand (and hence fisherman income) stability at the expense of foregone rents. The value judgements involved in making such multiobjective decisions can best be left to managers and politicians, but the analysis presented here provides a methodology for measuring losses in economic rents due to alternative (economically suboptimal) catch allocations between fleets in a sequential fishery.

Possible applications of the model to salmon and herring fisheries on the Pacific coast of Canada have been discussed previously. Problems of gear conflict are also prevalent on Canada's Atlantic coast. The general form of analysis presented here could be applied, for example, to the Newfoundland fishery on northern cod (*Gadus morhua*), where small inshore boats and large "factory-type" offshore vessels currently compete and coexist (Munro and McCorquodale 1981). This fishery has been well studied, but not yet within the context of a full bioeconomic optimization analysis. Inshore/offshore fisheries are common as well in developing countries, where typically the needs of small-scale domestic fishermen must be balanced with the benefits of agreements allowing distant water fleets to harvest local fish stocks (A. T. Charles, unpubl. data).

A full analysis of uncertainties, nonlinearities, and mixed stock problems may be required in order to determine the optimal fleet mix for specific real-world fisheries. Nevertheless the general results obtained here regarding coexistence, competition, and optimal catch allocation between inshore and offshore fisheries are likely to be quite robust in practice.

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Age and Growth of the Sandbar Shark (*Carcharhinus plumbeus*) from the Western North Atlantic[1]

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Age and growth of the sandbar shark (*Carcharhinus plumbeus*) was determined from rings in the vertebrae of 475 individuals, tagging data from 220 sharks at liberty for up to 17 yr, and length–frequency data from 2594 individuals. The oldest male sandbar aged in this study was 15 yr old and 154 cm fork length (FL); the oldest female was 21 yr old and 204 cm FL. The sexes grew at similar rates, 5.2–7.3 cm/yr. Females reached a larger adult size. Age to maturity was estimated at 13 yr in males and 12 yr in females. Tag returns indicated that sandbar sharks may live for over 30 yr. von Bertalanffy parameters for males are $L_\infty = 257$, $K = 0.0501$, $t_0 = -4.5$ and for females are $L_\infty = 299$, $K = 0.040$, $t_0 = -4.9$.

L'âge et la croissance du requin gris (*Carcharhinus plumbeus*) ont été déterminés à l'aide des anneaux vertébraux chez 475 individus, de données d'étiquetage recueillies chez 220 requins en liberté jusqu'à 17 ans et de données sur la fréquence des longueurs de 2 594 spécimens. Le plus vieux mâle était âgé de 15 ans et avait 154 cm de longueur à la fourche (LF) tandis que la plus vieille femelle avait 21 ans et mesurait 204 cm LF. Les taux de croissance étaient semblables chez les deux sexes, soit de 5,2 à 7,3 cm/an. À l'état adulte, la femelle atteinte une plus grande taille. L'âge à la maturité est de 13 ans chez les mâles et de 12 ans chez les femelles. Les étiquettes récupérées révèlent que le requin gris peut vivre plus de 30 ans. Les paramètres de von Bertalanffy ont les valeurs suivantes : pour le mâle $L_\infty = 257$, $K = 0{,}0501$ et $t_0 = -4{,}5$; pour la femelle $L_\infty = 299$, $K = 0{,}040$ et $t_0 = -4{,}9$.

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The sandbar shark (*Carcharhinus plumbeus* Nardo) is a worldwide species in tropical and subtropical regions of the Pacific, including the Hawaiian Islands (Tester 1969), the East China Sea (Taniuchi 1971), the Indian Ocean (Bass et al. 1973), the eastern and western Atlantic (Bigelow and Schroeder 1948), and the Mediterranean Sea. Garrick (1982) provided details on the distribution and taxonomy of *C. plumbeus* in a recent revision of the genus.

The sandbar shark was the most abundant species in the commercial shark fishery along the United States east coast during the 1940's and 1950's (Springer 1960). Although current United States commercial landings of sharks are low, the sandbar shark ranks second among all species of large sharks caught by American anglers (Casey and Hoey 1985). Springer (1960) provided excellent insights into sandbar life history but little is known about its age or rate of growth. Springer discussed the possibility of rapid growth (2–3 yr) to maturity (150 cm fork length (FL)) based on his length–frequency data. Wass (1973) reported age at maturity to be between 3 and 13 yr for Hawaiian specimens, and Lawler (1976) estimated sandbar shark ages up to 28 yr based on limited examination of rings in the vertebrae. None of these studies attempted to verify the formation of annual rings.

Validation of growth marks as year marks is vital in developing reliable ageing techniques that are useful to fisheries managers. In 1759, Hederström (translated in 1959) developed criteria for defining year marks that include the essential elements later elaborated on by many authors. Lagler (1956) provided an overview on the subject. We have attempted to verify our age results by examining marginal increments, vertebrae from tagged and recaptured sandbar sharks, and aquarium-held specimens. Age determination of large sharks is more difficult than that of bony fishes primarily because of the absence of cyclic marks on scales, otoliths, or fin rays. In addition, biologists seldom have the opportunity to tag or obtain samples of large sharks over the size ranges and time required for age studies. Consequently, few age studies adequately deal with large sharks; those that do include Olsen (1954), Aasen (1963), Stevens (1975), Thorson and Lacy (1982), and Pratt and Casey (1983).

We report here age estimates and measures of growth rate for the sandbar shark based on interpretations of rings in the vertebrae, results of tag and recapture data, and analysis of length–frequency data. This study was carried out as a contribution to the MARMAP program of the Northeast Fisheries Center, which is concerned in part with defining the role of pelagic sharks in the shelf ecosystem off the northeast coast of the United States.

Materials and Methods

Our main sources of sharks for tagging, obtaining vertebral samples, and length–frequency measurements came from a

[1]MARMAP Contribution MED/NEFC 82-1.

commercial shark fishery in Great Machipongo Inlet, VA (1965–69), and from research cruises and sport fishing tournaments in the Mid-Atlantic Bight (1965–81). Sampling covered all but a few winter months and was most intensive from May to September. Total and fork lengths were measured to the nearest centimetre following the conventions of Bigelow and Schroeder (1948). All lengths are reported as fork lengths unless otherwise noted. Fork lengths (FL) can be converted to total lengths (TL) using the regression FL = 0.8265 TL + 1.3774, $R^2 = 0.99$, $N = 4250$. Other sharks including tagged specimens were provided by fishermen, and two individuals maintained at the New England Aquarium were made available for our studies. With the exception of the two largest females, this paper concerns specimens taken from the area between Cape Hatteras and Cape Cod. The largest females (210 and 212 cm FL) were captured during a research cruise off northeastern Florida, and back-calculations from their vertebrae are included in the data base. The 212-cm female (241 cm TL) is near the maximum size reported for the species (Garrick 1982).

Vertebral Samples

The 15th through 20th vertebrae were chosen for age analysis in anticipation of their accessibility in commercially processed sharks. During commercial handling of sharks, the head is usually removed by severing the spinal column at the first gill opening. This is the approximate location of the 15th vertebrae in the sandbar shark. Our samples were taken from whole sharks by removing the posterior part of the chondrocranium and the vertebral column back to the third or fourth gill opening. The first few vertebrae are embedded in the chondrocranium and these were counted to obtain numbers 15 through 20. The vertebral column was cleaned and then either dried, frozen, or preserved in 10% Formalin or Bouin's solution.[2]

The 19th and 20th vertebrae were processed histologically and one (usually the 20th) was sectioned for interpretation. Vertebrae in this region are relatively homogeneous and we used them interchangeably. Several techniques were tried to aid enhancement and interpretation of the rings in the vertebrae. These methods included simply counting rings on the face of dried or fresh vertebrae without any preparation, X-raying or staining whole vertebrae, and sectioning dried vertebrae with a jeweler's saw and then polishing the section. In all of these methods, rings were visible but were either difficult to measure precisely and/or showed poor agreement when counted by different readers. Histological techniques, although more involved and time consuming, produced the best results.

The histological technique used is a standard process for the preparation of calcified material (Humason 1972). We modified the method by substituting *tert*-butyl alcohol for xylene during the infiltration phase. This eliminated the problem of hardening and distortion of the decalcified tissue. Details of the procedure may be obtained from the authors. Although dried vertebrae can be rehydrated and decalcified for staining and/or sectioning (Lamarca 1966), they shrink and distort somewhat during drying. After comparing sections of dried versus preserved vertebrae, we elected to use only preserved material.

Individual vertebrae were trimmed prior to decalcification by removing approximately one third of the dorsal and ventral portions with a hacksaw. The central portion of the centra (approximately 3–10 mm thick) was decalcified by soaking in 50× their volume in commercially prepared decalcifying solutions such as Decal and Cal-Ex II from 12 h to 5 d, depending on thickness and density of the tissue. The tissue was then washed overnight in running tap water and processed in an Autotechnicon. The embedded centra were sectioned in the frontal plane with a sledge microtome to obtain 80- to 100-μm sections from the center of the centra. The focus of the section was determined by the presence of the notochordal remnant (funiculus chordae; Fig. 1). Five to 10 sections were obtained from each vertebra.

Some sections were mounted on glass slides without staining; others were progressively stained in Harris's or Gill's hematoxylin and mounted in von Apathy gum syrup (Humason 1972). The pH of the mounting media was made slightly basic with the addition of ammonium hydroxide or sodium hydroxide to prevent the hematoxylin from fading or changing color. Sections prepared using this method showed no perceptible shrinkage and only minor color changes after 15 yr.

Sections (Fig. 1) were "read" using a dissecting microscope at 10× magnification with transmitted light. Measurements were made with an ocular micrometer positioned to measure distances from the notochordal remnant (focus) to growth bands at points along the internal margin of the corpus calcareum. The radius of each centrum was measured from the focus to the distal margin of the intermedialia. We attempted to define criteria for cyclic mark identification on the basis of cell morphology and examined sections at magnifications of up to 1250×. We also tried different stains and compared a variety of cross and longitudinal sections at high magnification. Although the cells in the opaque zones are more compressed than those in the translucent zones, we found no consistent cellular differences which would separate "checks" from what we believed to be yearly growth bands.

Our criteria to define an annual growth mark required that the mark must occupy a distinct narrow opaque zone relative to wider adjacent translucent zones in the intermedialia, and that the mark must traverse the entire intermedialia and clearly extend into the corpus calcareum (Fig. 1). Other marks were considered to be either checks or prebirth marks. Prebirth marks, designated A and B, were faint marks observed on 10 and 34%, respectively, of the total sample.

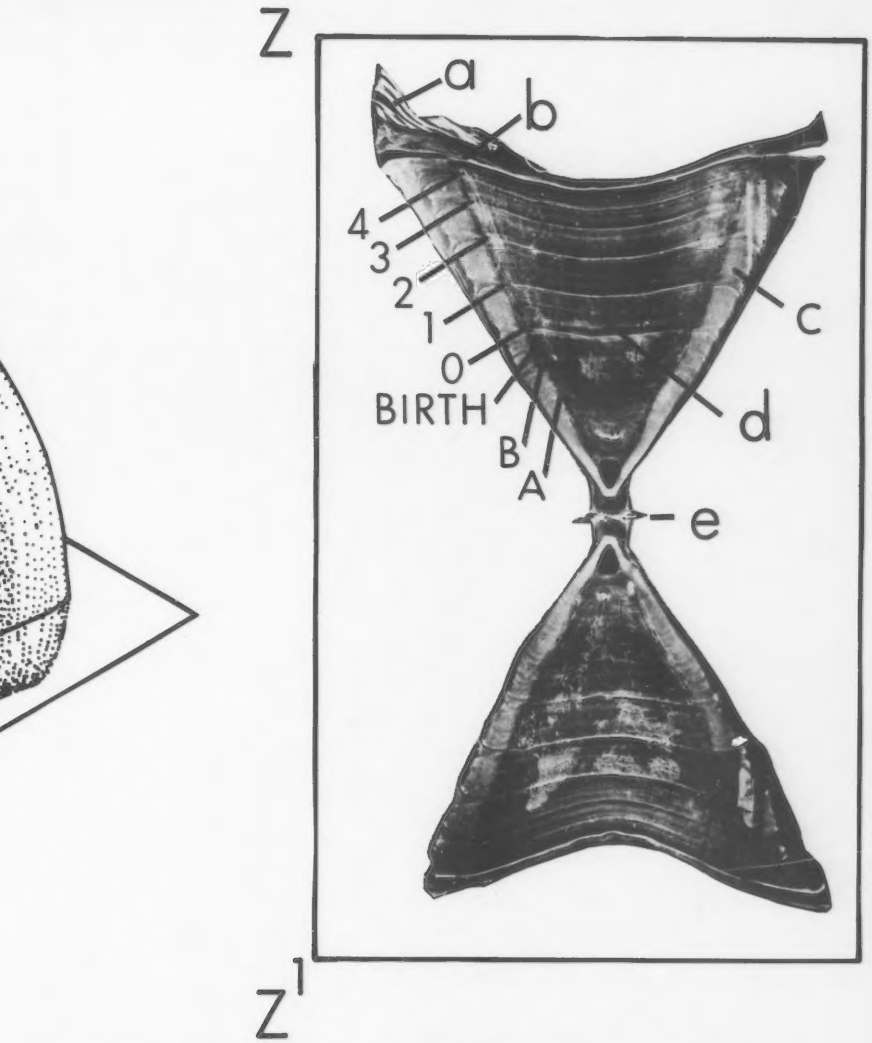
The birth mark was defined as the first distinct mark distal to the focus that coincided with a change in the angle of the corpus calcareum. The next mark was designated "0" and interpreted to be the first winter mark, representing an average of 6 mo of growth from June to January. Mark 1 was considered the next winter mark (i.e. 18 mo from birth) and marks 2, 3, 4, etc., succeeding winter marks.

Vertebral sections from 535 sandbar sharks were prepared. The same section from each centrum was read at least once by each author and the data recorded on a computer form that included a series of comments for rating the overall quality of the section. The comments ranged from "unreadable" to "excellent clarity." If the three readers disagreed by more than one band, the data were considered in poor agreement and the shark was deleted from the sample. In a few cases, sections from previously deleted large sharks were reread because of the small sample size in the older age groups. The measurements to each mark were averaged among readers and used to back-calculate size at age.

Of the 535 vertebrae examined, 60 (11%) were deleted as "unreadable," "poor agreement" among the three readers, "distorted," or "partially read." The latter category referred to

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIG. 1. Branchial vertebra and longitudinal section used for age determination. A, B = p
calcareum; d = intermedialia; e = notochordal remnant; Z–Z^1 = plane of section (terminol



, B = prebirth mark; 0, 1, 2, 3, 4 = year marks; a = membrane elastica externa; b = margin, c = corpus
terminology follows Ridewood 1921).

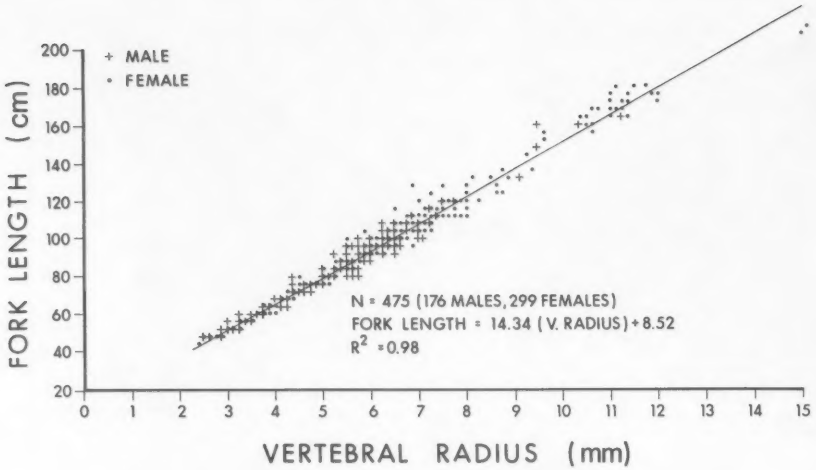


FIG. 2. Relationship between vertebral radius and fork length in *C. plumbeus*.

large vertebrae on which only the first few bands could be interpreted. Readings from the remaining 475 individuals were retained for back-calculation.

Vertebral readings were back-calculated by the Dahl–Lea direct proportion method (Lagler 1956) using the following equation:

$$FL_n = (FL_c/VR_c)(VR_n)$$

where FL_n = calculated fork length at mark n, FL_c = fork length at capture, VR_c = vertebral radius at capture, and VR_n = vertebral radius to mark n (i.e. distance to each yearly growth mark).

This method does not include a correction factor to account for growth of the embryo before the vertebrae are formed. We felt its use was justified because embryonic growth (Springer 1960) is more rapid than adult growth and constitutes a different growth stanza (Ricker 1979). Our vertebral samples include only full-term embryos, and the back-calculations, therefore, best describe growth from birth to maturity.

To determine how many vertebral rings are formed each year, we compared the number of rings present in a recaptured shark's vertebral centrum with the number of vertebral rings expected (predicted) for each year the shark was at liberty. We also back-calculated length at tagging from the vertebrae of recaptured sharks that had been measured at tagging and recapture. If the back-calculated size agrees with the measured size at tagging then this is strong evidence that (1) the rings are annual and (2) the back-calculation method is justified. Since we did not actually mark the vertebrae at tagging (e.g. with a flurochrome stain), our analysis may be considered verification rather than validation of annual rings.

Tagging Data

From 1963 through 1981, approximately 5000 sandbar sharks were tagged with cattle ear tags (rototags) or with modified "M" dart tags (Davies and Joubert 1967) and released under the NMFS Cooperative Shark Tagging Program. The "M" tags were used primarily by sport and commercial fishermen who implanted the tag using a 1- to 2-m tagging pole, and estimated the shark's size without removing it from the water. Rototags were used by the authors when operating with commercial shark fishermen or on research cruises where sharks were measured accurately before release.

Tags were returned primarily by sport and commercial fishermen who usually reported the size in total length or weight. All measurements and estimates were converted to fork length.

Aquarium Specimens

We measured and tagged a 92-cm male sandbar shark in 1974 at the New England Aquarium that we subsequently measured in 1979, and again when it died in 1981. We also measured and tagged a 137-cm female in 1979 that died in 1981. Both specimens were maintained in a circular 681 000-L tank (12 m high × 7 m in diameter). Seawater from Boston Harbor is added to the system to maintain a temperature which in a normal year ranges from a monthly mean of 27°C in July to as low as 22°C in January. The sharks were fed all they would eat once daily; however, they commonly refused food for 2- or 3-d periods (G. Early, New England Aquarium, Boston, MA, pers. comm.).

Results

Analysis of covariance showed no difference between the regression of fork length on vertebral radius between sexes; therefore, these data were combined into a single regression. A highly significant linear relationship was found between fork length and vertebral radius for male and female (combined) sandbar sharks ($r^2 = 0.98$, $N = 475$) (Fig. 2). Growth of the sandbar shark is slow and fairly constant. The only difference between males and females as reflected in the back-calculations is the attainment of a greater size by the females (Fig. 3; Table 1).

Since Lee's phenomenon was not pronounced, a von Bertalanffy growth function was fit to the back-calculated estimates using the nonlinear Biomedical Computer Program BMD PAR. The best compromise between an acceptable L_∞ and relatively low residual sum of squares was reached by deleting the last three points from the back-calculated females because of low sample size and extraordinary growth. The entire male data set

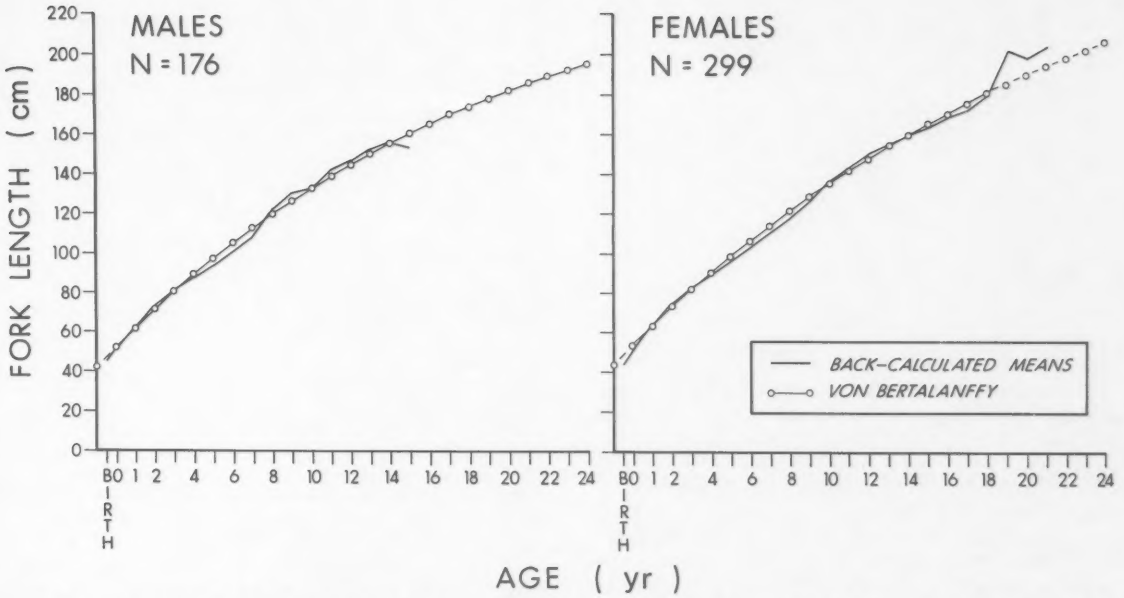


FIG. 3. Estimated growth of *C. plumbeus* from back-calculations of rings in the vertebrae with a von Bertalanffy growth curve for back-calculated data. Males: $n = 176$, $K = 0.076$, $L_\infty = 204$ cm, $t_0 = -4$. Females: $n = 299$, $K = 0.057$, $L_\infty = 250$ cm, $t_0 = -5$.

TABLE 1. Estimated fork lengths (cm) of *C. plumbeus* at age from back-calculations of rings in vertebrae (B = birth; "0" = first winter).

	Ring (age in years)																					
	B	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Males																							
N	168	168	154	122	115	97	55	40	20	7	6	5	3	2	2	2	1						
Mean	45	51	63	73	81	88	94	100	107	123	130	132	142	146	152	156	154						
SD	3	3	4	4	5	5	6	7	10	11	12	9	5	7	9	9							
Females																							
N	283	286	276	248	236	214	187	139	92	62	46	34	32	28	22	16	10	10	7	5	2	1	1
Mean	44	52	65	75	83	90	97	104	111	118	127	137	144	151	155	160	164	169	173	180	202	199	204
SD	3	4	5	4	5	5	6	7	8	9	10	9	10	10	8	6	8	10	13	15	8		
Sexes combined																							
N	451	454	430	370	351	311	242	179	112	69	52	39	35	30	24	18	11	10	7	5	2	1	1
Mean	44	52	64	74	82	90	96	103	110	119	128	136	144	151	155	160	163	169	173	180	202	199	204
SD	3	4	5	5	5	6	7	8	9	9	9	9	10	8	6	8	10	13	15	8			

was used; otherwise, mature males would have been excluded. Best fits (Fig. 3) were obtained for males with $L_\infty = 257$, $K = 0.0501$, $t_0 = -4.5$ and for females with $L_\infty = 299$, $K = 0.040$, $t_0 = -4.9$.

Back-calculated growth of the male and female sandbar sharks reveal several inflections when plotted. The curves (Fig. 3) are typical of asymptotic growth until 100–110 cm FL is reached. Both sexes then grow at a slightly greater relative rate until 150 cm, when growth again slows. This phenomenon is consistently present in individual sharks.

Time of Ring Formation

To determine time of vertebral ring formation the back-calculated mean increase in fork length from the last ring to the margin of the centrum was determined for the more numerous ($n = 438$) summer samples. Increments were as follows: June, 2.9 cm; July, 4.3 cm; August, 4.5 cm (Table 2). This increase represents a growth rate in the 2-mo period from mid-June to mid-August of 0.8 cm/mo. The mean annual growth for a 95-cm sandbar shark is about 6.0 cm based on back-calculations from vertebrae and tagging data (Tables 1 and 3). Growth of 4.5 cm by mid-August computed from marginal increments accounts for 75% of the estimated annual growth of 6.0 cm. By this interpretation, growth from mid-August to January 1 would be 0.33 cm/mo and from January 1 to mid-June 0.53 cm/mo. This progression of incremental growth rates when compared with mean annual growth suggests that one ring is formed each year between September and June with January a convenient, if somewhat arbitrary, midpoint.

TABLE 2. Estimated seasonal growth of *C. plumbeus* based on back-calculations of marginal increments on vertebrae. Males and females combined, n = 438; mean fork length 95.4 cm; LL = lower limit; UL = upper limit.

Month	Number	Mean growth in fork length (cm)	SD	SE of mean	C.I. (95%) LL	C.I. (95%) UL
June	178	2.89	2.2	0.17	2.63	3.13
July	54	4.26	2.6	0.36	3.44	4.88
August	206	4.46	2.4	0.17	4.02	4.70

Growth Data from Tagged and Recaptured Sharks

Our samples included vertebrae from six juvenile females that were measured when tagged and recaptured at Great Machipongo, VA (1–5 yr at liberty). Vertebral sections from these sharks showed distinct marks that agreed in all cases with one ring per year for the number of years between tag and recapture (Fig. 4). The sharks were recaptured in May (1), June (4), and August (1), and showed mean back-calculated growth of 2.3 cm from the last ring to the margin for those recaptured in May and June, and 5.0 cm for the individual recaptured in August.

A vertebral sample was also obtained from a male sandbar shark tagged at a reliably estimated length of 102 cm, and recaptured and measured at 152 cm 8 yr later (see M 21897, Table 4). Interpretation of the vertebral section from this individual indicated an age of 14 yr with eight growth bands between the back-calculated length at tagging and length at recapture (Fig. 5).

Aquarium Specimens

Despite controlled water conditions and almost unlimited food, growth bands in the vertebrae of the two sandbar sharks held in the New England Aquarium were indistinguishable from those found in the natural population. Seasonal cues provided by the addition of seawater and variation in light levels may explain the presence of growth bands in these captive sharks. The number of bands between the time they were measured and died agreed with our interpretation of one band per year and provided evidence of seasonal growth in captive sharks. Growth curves for these two individuals based on interpretation of rings in the vertebrae agree closely with the mean back-calculated values for the natural population (Fig. 5).

A distinctive characteristic in the aquarium sharks was an indentation in the corpus calcareum of both specimens between rings 5 and 6 (Fig. 6). This feature was not observed on any vertebrae from sandbar sharks collected in the field, and the irregularity in the vertebrae of captive sharks may have been caused by the addition of chemicals to control parasites in the aquarium (see Discussion).

Tag Returns

A total of 220 tagged sandbar sharks were recaptured between 1964 and 1982. An effort was made to extract the best possible growth information from these sharks for comparison with back-calculations. Forty-four of the 220 sharks recaptured were not measured at some point (either recapture or tagging). One hundred and twenty-eight sharks were returned with lengths or weights estimated at tagging and/or recapture. The remaining 48 measured sharks were analyzed for growth information (Table 3). Sharks at liberty for less than 1 yr were eliminated because measurement error on short-term recaptures became magnified when displayed as growth per year. The remaining 22 sharks were arranged in 20-cm size groups. Growth from 50 to 109 cm was 5.5 to 5.9 cm/yr (Table 3). Slopes of these growth rates agree well with back-calculations for these size ranges.

In addition, growth indicated by 32 of the recaptures from sharks whose lengths were estimated at tag or release agreed closely with measured values and provided information on growth of larger sharks after they had moved offshore (Table 4). These were selected from the 128 sharks whose lengths were estimated at return by including only those individuals whose annual growth rate fell within three standard deviations of the mean annual growth rate for the measured fish. The range in yearly growth of 32 sharks at liberty from 1 to 17 yr was 0 to 13.3 cm with a mean of 5.4 cm/yr.

Length–Frequency

Length–frequency data yield clearest polymodality when all years from the Machipongo commercial shark fishery are grouped by sex (Fig. 7). Back-calculated means from Table 1 are graphed to compare results of the two methods. The major length–frequency peaks agree well with the back-calculations. Size estimates for years 3, 4, and 5 align well with the males' peaks, and years 4, 5, 6, and 7 align well in the females' peaks. Other peaks and means line up but with less definition or exactness because of overlapping of modes or a paucity of samples due to gear selectivity and population distribution.

Discussion

Analysis of growth zones in vertebrae, growth of aquarium specimens, length–frequencies, and tagging data provides compelling evidence that the sandbar shark is a long-lived, slow-growing species. However, despite the close agreement of the age and growth estimates based on the above methods, there are shortcomings in the use of any one of them as the sole means for ageing large sharks.

There is a slight trend for Lee's phenomenon in back-calculations derived from older fish for ages birth, "0", and 1. This is probably due to the selectivity of the gillnet fishery which supplied about half the vertebral samples.

In attempts to age most fish from hard parts the centrum rings of the larger and/or older individuals are the most difficult to interpret. We found this particularly true in adult sandbar sharks even on vertebral sections that were exceptionally clear. In order to include data from adults we reread sections from large specimens on which our initial counts were not in complete agreement. The second series of readings produced closer agreement on some sections, but it was difficult to adhere rigidly to criteria because of the large number of rings near the margin that could be interpreted as year marks. If these, indeed, prove to be year marks in future studies, then our maximum counts of 15 yr for males and 21 yr for females are underestimates.

Another possible source of error in reading vertebrae is in distinguishing between the birth ring and the first winter mark (Fig. 1). A change in angle in the corpus calcareum at about the size at birth was clearly evident in some vertebrae, less so in others. The mean back-calculated length for the sandbar shark at birth was 44.2 cm, which is slightly below the mean length (47.7 cm) of the measured embryos that were near full term. The lower size estimates from back-calculations in smaller sharks,

TABLE 3. Tag returns from *C. plumbeus* measured at tagging and recapture (at liberty from 30 d to 15 yr) (YR = yellow rototag; RR = red rototag; M = "M" dart tag).

Size class (cm)	Tag type	Tag No.	Sex	Date (d/mo/yr)		Days free	Fork length (cm)			Growth per year	Mean growth per year	SD
				Tag	Recapture		Tag	Recapture	Growth			
	RR	1001	F	6/16/66	7/16/66	30	93	95	2	—		
	RR	945	M	6/15/66	7/16/66	31	71	77	6	—		
	YR	2209	M	8/29/80	10/06/80	38	55	55	0	—		
	RR	1086	F	7/28/66	9/05/66	39	102	103	1	—		
	YR	2249	F	9/14/80	10/28/80	44	69	69	0	—		
	RR	775	U	6/23/65	8/08/65	46	85	94	9	—		
	YR	480	M	6/18/66	8/04/66	47	91	98	7	—		
	RR	966	F	6/15/66	8/06/66	52	80	86	6	—		
	RR	779	F	6/23/65	8/15/65	53	84	86	2	—		
	RR	785	M	6/23/65	8/15/65	53	104	115	11	—		
	YR	379	M	6/17/66	8/10/66	54	88	92	4	—		
	RR	672	F	6/20/65	8/15/65	56	103	104	1	—		
	M	70265	F	8/13/80	10/12/80	60	53	53	0	—		
	YR[a]	120	F	7/16/65	9/16/65	62	48	51	3	—		
	YR	541	F	7/06/66	9/06/66	62	101	107	6	—		
	YR	522	F	7/05/66	9/06/66	63	93	98	5	—		
	YR	400	M	6/18/66	9/10/66	84	87	94	7	—		
	M	24450	M	3/09/75	6/01/75	84	67	69	2	—		
	M	55977	U	10/07/79	1/03/80	88	61	67	6	—		
	YR	408	F	6/18/66	3/29/67	284	83	89	6	—		
	M	41610	F	7/29/78	5/27/79	302	102	104	2	—		
	RR	176	M	7/22/64	6/01/65	314	92	94	2	—		
	YR	255	F	8/06/65	6/23/66	321	107	115	8	—		
	YR	722	F	6/26/67	6/03/68	343	94	101	7	—		
	RR	199	M	7/28/64	7/11/65	348	88	109	21	—		
	RR	769	M	6/23/65	6/17/66	359	81	92	11	—		
50–69	YR	128	M	7/16/65	8/17/67	762	63	75	12	5.8	5.2	0.7
	RR[a]	951	F	6/15/66	5/08/68	693	69	78	9	4.7		
70–79	RR	995	M	6/16/66	8/25/67	435	74	83	9	7.6	5.5	2.9
	RR[a]	747	F	6/22/65	6/18/70	1822	80	99	19	3.8		
	RR	410	F	6/19/65	6/22/70	1829	81	106	25	5.0		
	YR	1373	M	6/09/69	6/21/71	742	83	103	20	9.8		
	RR	219	M	7/29/64	5/28/68	1399	86	89	3	0.8		
	YR[a]	471	F	6/18/66	6/16/69	1094	86	98	12	4.0		
	RR	798	M	6/23/65	8/08/67	776	88	98	10	4.7		
	RR	930	F	6/25/65	8/25/68	1157	89	115	26	8.2		
90–109	YR	1219	F	8/10/68	7/05/70	694	91	102	11	5.8	6.0	2.8
	YR[a]	330	F	6/17/66	6/20/67	368	92	95	3	3.0		
	RR	962	M	6/15/66	8/08/73	2611	93	138	45	6.3		
	RR	714	M	6/22/65	9/12/66	447	94	102	8	6.5		
	YR	884	M	8/01/67	8/28/68	393	95	101	6	5.6		
	RR[a]	894	F	6/24/65	8/05/68	1138	95	112	17	5.5		
	YR[a]	375	F	6/17/66	6/26/67	374	101	105	4	3.9		
	RR	435	F	6/20/65	8/31/66	437	101	111	10	8.4		
	RR	758	M	6/22/65	10/04/66	469	102	118	16	12.5		
	RR	369	F	6/19/65	8/25/68	1163	104	114	10	3.1		
150–169	M	19399	F	3/13/73	3/27/76	1110	164	168	4	1.3	1.3	—
170–189	M	3030	M	9/26/66	11/20/76	3708	185	176	−9	−0.9	−0.9	—

[a]Measured at tagging and recapture by authors (others measured by authors or fishermen). Vertebrae were examined from the six largest sharks measured by the authors.

in this case at birth, and the first winter mark may be due in part to Lee's phenomenon. Another explanation is that our defined "birth mark" was laid down in utero just prior to birth. However, the 7.5 cm of growth between birth and the "0" mark compares well with the tag return and length–frequency data.

The rate of growth for the sandbar shark is more constant than is typical of fishes. Our back-calculated estimates, which are well supported by tag–recaptures, do not display the consistent "slow down" usually present in asymptotic growth data. Each resultant low K value generates an artificially high L_∞ and an unreasonably large t_0 (−4.5, −4.9). Gestation time is known to be about 1 yr in the sandbar shark (Springer 1960).

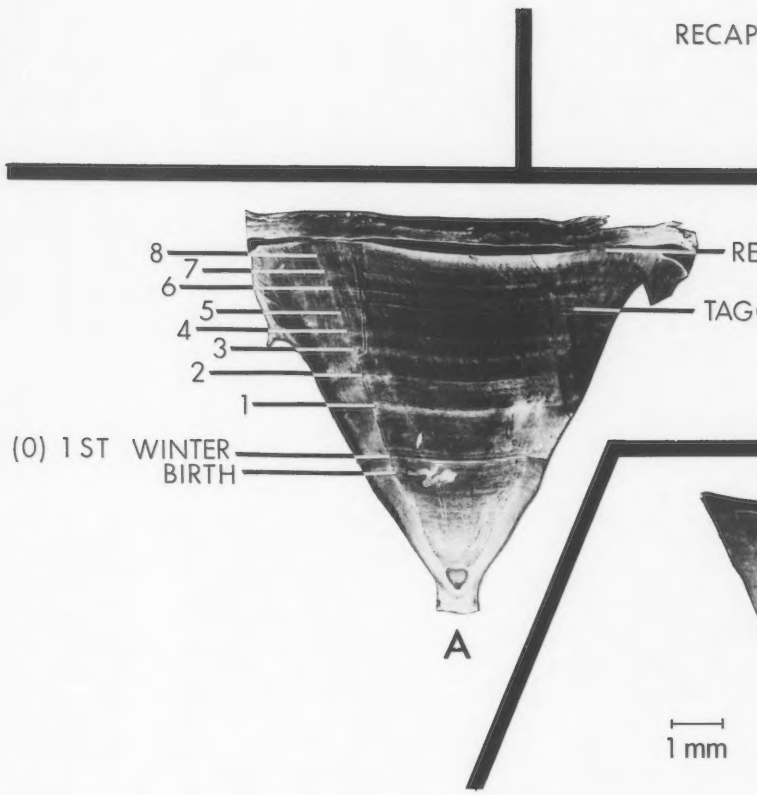
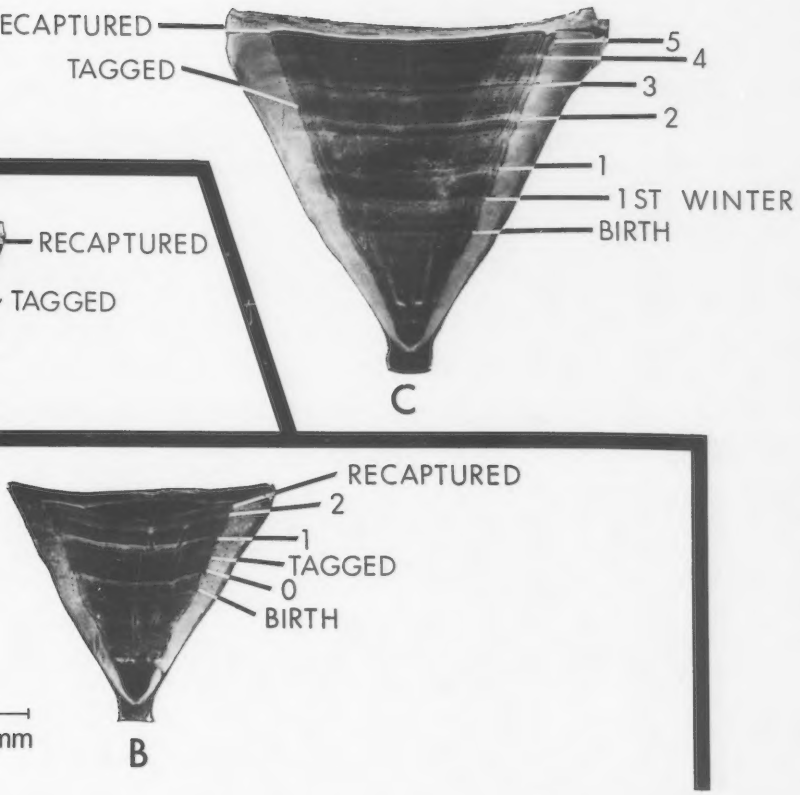


FIG. 4. (A) Vertebral section from tagged *C. plumbeus* recaptured after 1138 d (June 1965 – A
section from tagged sandbar shark recaptured after 693 d (June 1966 – May 1968). The shark w
plumbeus recaptured after 1094 d (June 1966 – June 1969). The shark was tagged after winter m



965 – August 1968). The shark was tagged after winter mark at 5 was formed in 1965. (B) Vertebral shark was tagged after winter mark at "0" was formed in 1966. (C) Vertebral section from tagged *C*. winter mark at 2 was formed in 1966.

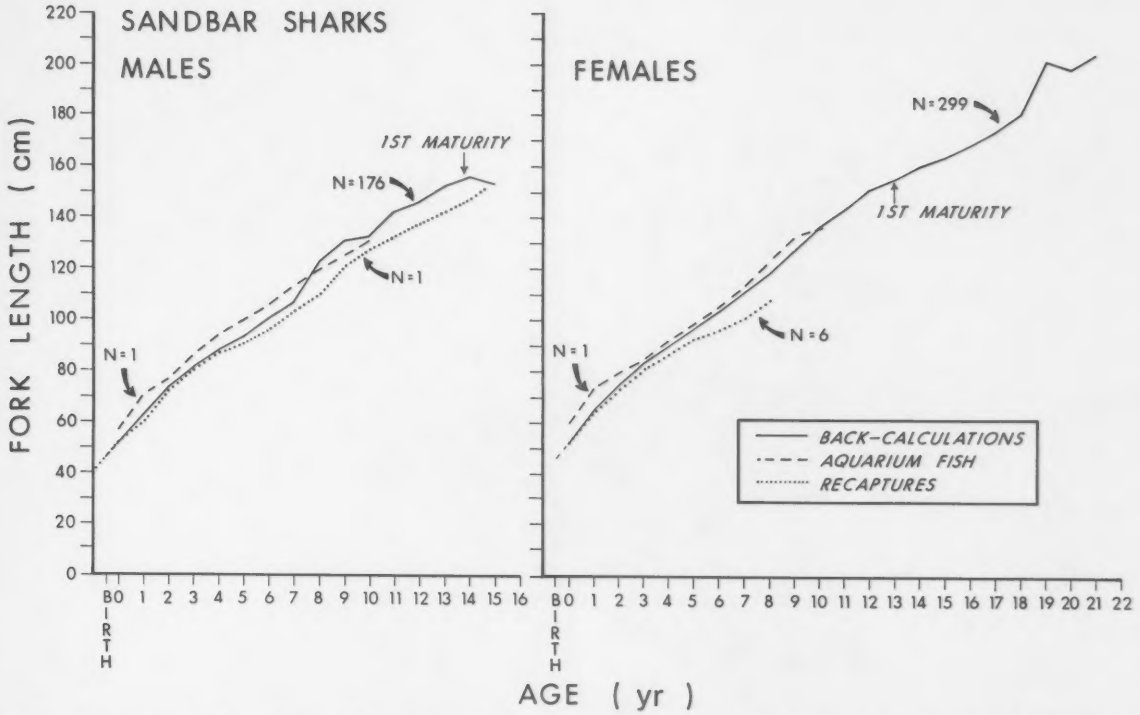


FIG. 5. Growth estimates from back-calculation of annuli in vertebrae of *C. plumbeus*. Aquarium sharks were held in the New England Aquarium for 3–6 yr. Recaptures came from tagged sharks at liberty from 1 to 5 yr.

Vertebral sections from embryos did not show a mark on the margin or show the prebirth marks that were visible on sections from larger sharks. Calcification is probably necessary for their disclosure. The prebirth marks designated A and B in Fig. 1 were visible on 10 and 34% of the total sample. The mean back-calculated fork length for embryos at prebirth rings A and B was 32 and 38 cm, respectively. Springer's (1960) observations on the embryology of the sandbar shark offer one explanation for prebirth rings. He suggested three sources of nutrient material for the embryo, with early growth provided by egg yolk and fluids in the oviducts and later growth by the pseudoplacenta. He estimated that the pseudoplacenta forms from the yolk sac when the embryos are approximately 25 cm long and that the yolk is completely absorbed when they reach 31 cm. Although his estimates are lower than our back-calculated values, the change in nutrient sources could account for the prebirth marks. These marks could also reflect migrations and/or winter marks of the mother.

Attempts to establish a precise relationship between marginal increments and season in slow-growing sharks will often produce questionable results. The area of greatest uncertainty for interpreting and measuring growth zones in sandbar shark centra is near the margin. The presence of the last ring is difficult to determine and the authors could not always agree on whether or not a ring was forming on the margin. It is a common problem in interpreting scales and other hard parts that the last ring is not discernible until additional marginal growth has taken place. Consequently, the same vertebral section can sometimes be interpreted as either lacking a marginal increment (i.e. last ring forming) or having a broad marginal increment (i.e. last ring not discernible). The difficulty in distinguishing the last ring may account for the relatively high SD values in Table 2. Nevertheless, it is not unreasonable from the available evidence to designate January as the month when the annual ring is formed.

Sandbar sharks held in the New England Aquarium for up to 6 yr provided indirect evidence that marks in the vertebrae are influenced by external conditions. In 1975, a tank containing two sandbar sharks was treated with a mixture of copper sulfate and citric acid to control parasites. Copper concentrations were maintained at 0.15 μg/L from late January to mid-March. During this period the sharks showed obvious behavioral changes of increased and agitated swimming and an inability or refusal to feed (G. Early, pers. comm.). The vertebrae of these sharks showed a distinct morphological change at about the time the water was treated (Fig. 6). Whether the water treatment was the cause of the distortion in the vertebral section is uncertain. However, that both vertebrae show a similar pattern suggests that in the sandbar shark, vertebral marks are influenced by environmental phenomena rather than being the result of an endogenous cycle for strengthening the vertebrae as suggested by Ridewood (1921) in the basking shark.

At 95–100 cm, sandbar sharks move from inshore nursery grounds to a year-round offshore existence. This shift offshore coincides with an increase in growth in some vertebrae, which is best illustrated in back-calculations from the vertebrae of recaptured sharks. The back-calculated growth curves from these sharks (Fig. 5) show a reduced growth rate for the females, all of which were tagged and recaptured at Great Machipongo. The back-calculated values for the male, tagged at Great Machipongo and recaptured 8 yr later in the Gulf of Mexico,

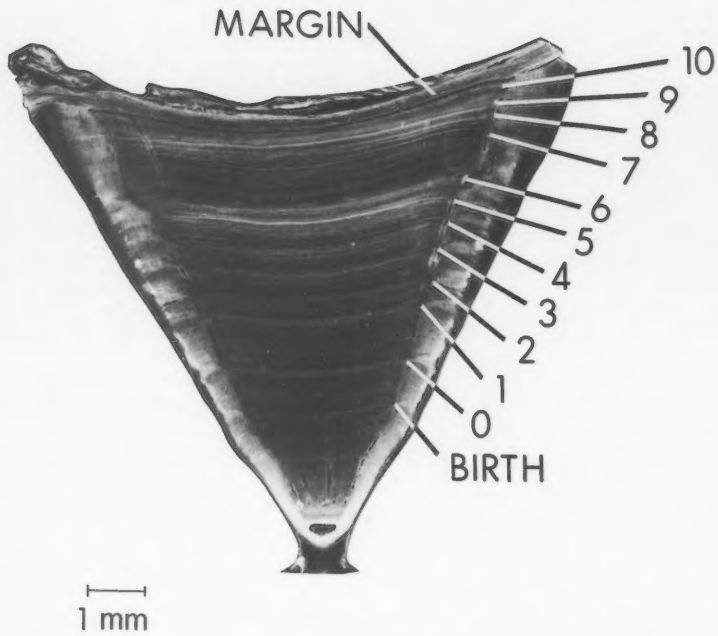
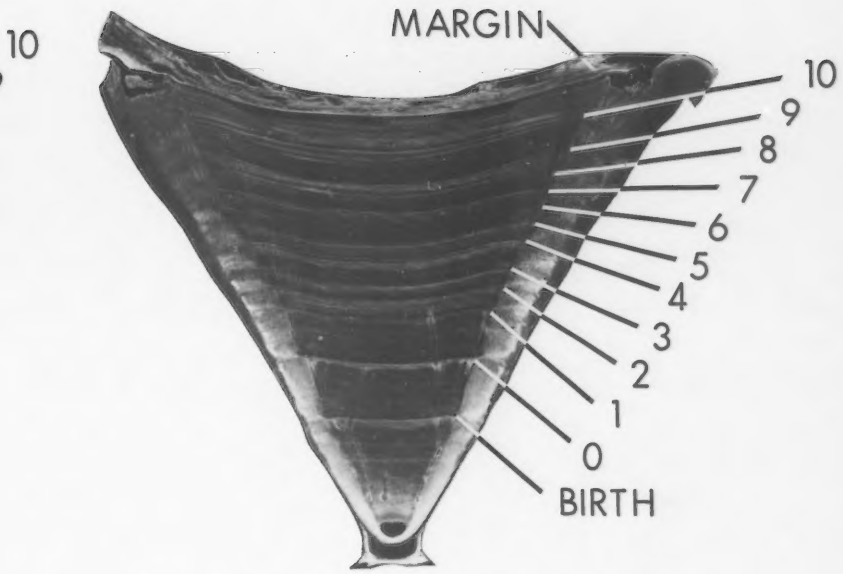


FIG. 6. Vertebrae from *C. plumbeus* held in the New England Aquarium for several years. S
1981. Section at left is from a male that grew from 93 to 134 cm from August 1974 to Janua



l years. Section at right came from a female that grew from 137 to 144 cm from September 1979 to February to January 1981. Both sections show angle change at rings 5 and 6 referred to in text.

TABLE 4. Tag returns from *C. plumbeus* estimated at tagging and/or recapture (at liberty from 1 to 17 yr) (YR = yellow rototag; RR = red rototag; M = "M" dart tag; F = Floy tag).

Tag type	Tag No.	Sex	Date (d/mo/yr)		Days free	Fork length (cm)			Growth per year
			Tag	Recapture		Tag	Recapture	Growth	
YR	553	M	7/07/66	7/08/67	366	96[a]	107	11	11.0
M	61625	U	7/11/80	7/16/81	370	124	124	0	0.0
M	18383	U	6/17/73	7/19/74	397	90	102	12	11.0
M	60373	F	8/08/80	9/09/81	397	102	114	12	11.0
YR	143	M	7/17/65	8/20/66	399	64[a]	68	4	3.7
RR	647	M	6/14/66	8/02/67	414	79[a]	77	−2	−1.8
M	61541	M	11/15/79	8/10/81	634	149	172	23	13.3
M	50879	U	7/21/79	7/28/81	738	127	149[a]	22	10.9
RR	939	F	6/25/65	8/23/67	789	83[a]	86	3	1.4
RR	489	F	3/24/65	7/11/67	839	176	184[a]	8	3.5
M	41600	F	7/21/79	11/10/81	843	102	127	25	10.8
F	9994	F	5/19/69	2/17/72	1004	177	185[a]	8	2.9
YR	1602	M	11/05/75	9/07/78	1037	94[a]	102	8	2.8
RR	226	M	7/29/64	7/07/67	1073	84[a]	102	18	6.1
M	49431	F	8/27/78	8/05/81	1074	139	170[a]	31	10.5
RR	412	F	6/19/65	6/16/68	1093	164	177[a]	13	4.3
M	15585	F	7/24/77	10/20/80	1184	139	137[a]	−2	−0.6
M	20927	F	8/09/75	7/26/79	1446	115	141	26	6.6
RR	933	F	6/25/65	11/17/69	1606	100[a]	133	33	7.5
RR	1050	F	6/17/66	12/29/70	1656	82[a]	109	27	6.0
M	31169	U	8/14/76	8/06/81	1818	114	139	25	5.0
M	18626	U	8/18/74	5/11/80	2093	144	164[a]	20	3.5
RR	789	M	6/23/65	7/15/71	2213	103[a]	153	50	8.3
M	31047	F	6/27/76	9/24/82	2280	126	165	39	6.2
RR	225	F	7/29/64	12/03/70	2318	73[a]	115	42	6.6
M	1072	M	8/28/65	3/20/73	2761	164	156[a]	−8	−1.1
M	21897	F	7/13/74	6/11/82	2895	102	152[a]	50	6.3
M	14584	F	8/01/71	3/20/80	3154	90	152[a]	62	7.2
RR	487	F	3/24/65	4/07/74	3301	176	191[a]	15	1.7
RR	419	F	6/20/65	2/17/75	3529	91[a]	127	36	3.7
RR	693	M	6/22/65	9/15/80	5564	99[a]	139	40	2.6
RR	784	F	6/23/65	8/08/82	6255	92[a]	125	33	1.9

[a]Measured fork length or total length.

show a similarly slow growth rate for the first 6 yr and an increased rate during the next 3 yr. The differential growth rates could be related to the small number of vertebral samples from large sharks (Table 1) or sampling bias due to the commercial gill nets selecting for a high percentage of slow-growing individuals. A more intriguing possibility is that the slow down in growth rate on the inshore nursery grounds indicates that the sharks have reached a size at which food, oxygen, or a combination of factors have become limiting and this is the mechanism that triggers their shift to the offshore zone. Stevens (1984) suggested food to be limiting for blacktip sharks (*C. melanopterus*) around the island of Aldabra (Indian Ocean), and Pauly (1979) offered evidence that growth is influenced by the amount of oxygen that can be processed over the surface area of the gills.

Length–Frequencies

In the sandbar shark, separation of age classes from modes in length–frequency distributions is difficult because of slow growth and modal overlap. Even as juveniles between 3 and 8 yr old, individuals of the same size can represent several year classes. Our length data do not include many small sharks ("0" and 1 yr olds) because they passed through the commercial gill nets and analysis of length data from larger sizes is insufficient to clearly demonstrate modal progressions with season. However, the modes in the length–frequencies from Great Machipongo for June (all years combined) compare reasonably well with age estimates from vertebrae and tagging data (Fig. 7).

Juvenile sandbar sharks in the 90–138 cm range occur on the inshore nursery grounds both at Great Machipongo and offshore on the continental shelf off Long Island (Fig. 7). With the exception of gravid females, sandbar sharks larger than 140 cm apparently remain offshore away from the inshore summer nursery grounds occupied by individuals less than 90 cm (see Springer (1960) for information on wintering grounds). The length–frequency data suggest that the males begin to move offshore at a slightly smaller size (90 cm) than the females (100 cm). In general, both sexes have moved away from the inshore grounds by the time they are 7 yr old and about 110 cm long.

Tag Returns

The problem of accurately measuring even a relatively small shark prior to tagging, combined with the different measuring devices and methods used by fishermen who recaptured the sharks, are sources of error in determining growth-per-year estimates. Moreover, a small increase in length is magnified when growth-per-day from short-term returns is extrapolated to

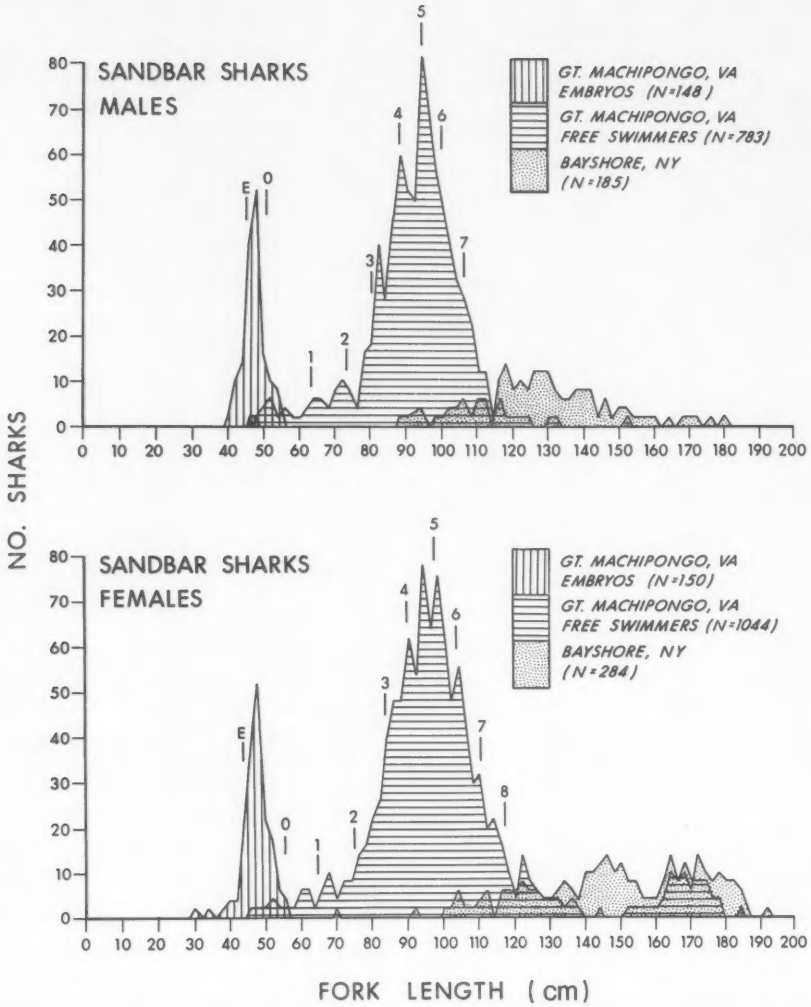


FIG. 7. Length–frequency distributions of male and female sandbar sharks (*C. plumbeus*) examined from the Mid-Atlantic Bight. Sharks were examined in June at Great Machipongo, VA, 1965–69, Bay Shore, NY, 1965–80, and off North Carolina in February 1958. The numbers above the frequency peaks indicate the mean back-calculated size at age from analysis of vertebrae.

express growth-per-year. Consequently, we considered returns from sharks that were measured at tagging and recapture, and were at liberty for over 1 yr, to be the most reliable data for determining annual growth.

Tag returns provide the most direct evidence of annual rings in vertebrae and support for our proposed growth curves based on predictive models. The following examples from recaptures in Tables 3 and 4 illustrate growth rates for different sizes and times at liberty. A 47-cm sandbar (tag YR 120), which was carefully measured by the authors at tagging and recovery, showed less than 3 cm of growth between mid-July and mid-September. Another shark (99-cm male) tagged by the authors at Great Machipongo (tag RR 693) was recaptured 15 yr later by a gillnet fisherman off Rhode Island. Although the fisherman did not measure the shark, it was one of 26 juvenile sandbar sharks he caught and sold on the same day. An examination of his weigh-out data and discussions with the fisherman established the best fork length estimate for this shark at between 130 and 148 cm. Since the minimum fork length at maturity in male sandbar sharks is 150 cm (Springer 1960), and mature male sandbar sharks are usually found segregated from juveniles, this individual may still have been immature at an estimated age of 23 yr. A recent return (tag RR 784) came from a 92-cm female measured at Great Machipongo in 1965 and recaptured 17 yr later near Campeche, Mexico. The reported length of 125 cm at recapture appears underestimated but assuming the shark had reached an average adult size of 175 cm it would still show a relatively slow growth rate of 4.8 cm/yr.

Individual recaptures from large sandbar sharks also show extremely slow growth. In September 1966 an adult male (tag M 3030) was caught from shore at Edisto Beach, SC. The shark was hauled to the beach, measured, tagged, photographed, and

released. Ten years later it was recaptured near Jacksonville, FL, and measured 9 cm shorter than when it was released. The photograph confirmed it was an adult male at tagging and its total length at recapture (223 cm) was only 2.5 cm less than the maximum reported size for males (Springer 1960). Assuming males mature at about 15 yr (Fig. 5), this individual was at least 25 and quite possibly over 30 yr old.

Acknowledgments

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Predicting Inshore Whale Abundance — Whales and Capelin off the Newfoundland Coast[1]

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Inshore abundance of baleen whales along the Newfoundland coasts changed considerably during the period 1973–83. In particular, large numbers of humpbacks were present along the northeast coast each summer between 1977 and 1980. This influx led to entrapment of whales in fishing gear. Counts of humpback (*Megaptera novaeangliae*), finback (*Balaenoptera physalus*), and minke (*Balaenoptera acutorostrata*) whales during standard surveys along the coast are used as indices of inshore abundance, and are related to the year-class strengths of capelin (*Mallotus villosus*), their major food in the Newfoundland region. Whales are found inshore when there are few immature capelin offshore. Minke whale distributions seem more closely related to the abundance of 1- to 2-yr-old, immature capelin, but humpback and finback whales are found inshore with low abundances of 2- to 3-yr-old, mainly immature capelin. We suggest that estimates of capelin year-class strength predicted from abiotic variables can be used to predict inshore whale abundance, at least 1 yr in advance. The extreme influx of humpbacks of the late 1970s is unlikely to recur in the short term. The analysis suggests that finback populations in the area are declining.

Le nombre de baleines à fanons dans les eaux côtières de Terre-Neuve a varié fortement de 1973 à 1983. En particulier, les rorquals à bosse étaient présents en grand nombres le long de la côte nord-est de 1977 à 1980, ce qui les amenaient à s'enchevêtrer dans les engins de pêche. Les dénombrements de rorqual à bosse (*Megaptera novaeangliae*), de rorqual commun (*Balaenoptera physalus*) et de petit rorqual (*Balaenoptera acutorostrata*) effectués au cours de levés normalisés le long de la côte sont utilisés comme indices de l'importance numérique en milieu côtier et sont mis en relation avec la biomasse des classes d'âge de capelan (*Mallotus villosus*), leur principale nourriture dans la région de Terre-Neuve. Les baleines fréquentent les eaux côtières quand il y a peu de capelans immatures dans les eaux hauturières. La répartition du petit rorqual semble étroitement liée à l'abondance de capelans immatures de 1 à 2 ans ; par contre, le rorqual à bosse et le rorqual commun occupent les eaux côtières quand le nombre de capelans de 2 à 3 ans, en grande partie immatures, est faible. Les auteurs formulent l'hypothèse que les estimations de la biomasse des classes d'âge de capelan extrapolées de variables abiotiques peuvent servir à calculer le nombre des baleines présentes dans les eaux côtières au moins 1 année à l'avance. L'abondance de rorquals à bosse signalée vers la fin des années 1970 ne se reproduira probablement pas à court terme. L'analyse porte à croire que les populations de rorqual commun sont en déclin dans cette région.

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During the summer months, humpback (*Megaptera novaeangliae*), finback (*Balaenoptera physalus*), and minke (*Balaenoptera acutorostrata*) whales are found off the Atlantic coast of Newfoundland, where they feed principally on capelin (*Mallotus villosus*) (Mitchell 1973, 1974a; Sergeant 1963). During the late 1970s the numbers of humpback whales along the northeast coast of Newfoundland in summer increased dramatically, and a large number of whales were entrapped in fishing gear, causing humpback mortality and considerable damage to the inshore fishermen (Lien 1981). In 1979, the worst year, 13 humpbacks died and the inshore fishery suffered about $2.5 million damage, approximately 2–3% of its total worth (Lien 1981). Since 1980, the situation has returned to pre-1977 levels, with relatively few whales inshore, and only moderate damage by whales to fishing gear.

Sergeant (1963) and Whitehead et al. (1980) presented evidence that the baleen whales change their geographic distributions, on a scale of days and weeks, in response to changing capelin abundance. Capelin were therefore a prime suspect in the search for a cause of the humpback influx of the late 1970s.

Capelin are small (approximately 13 cm) schooling fish. In the Newfoundland region they spawn on beaches or offshore

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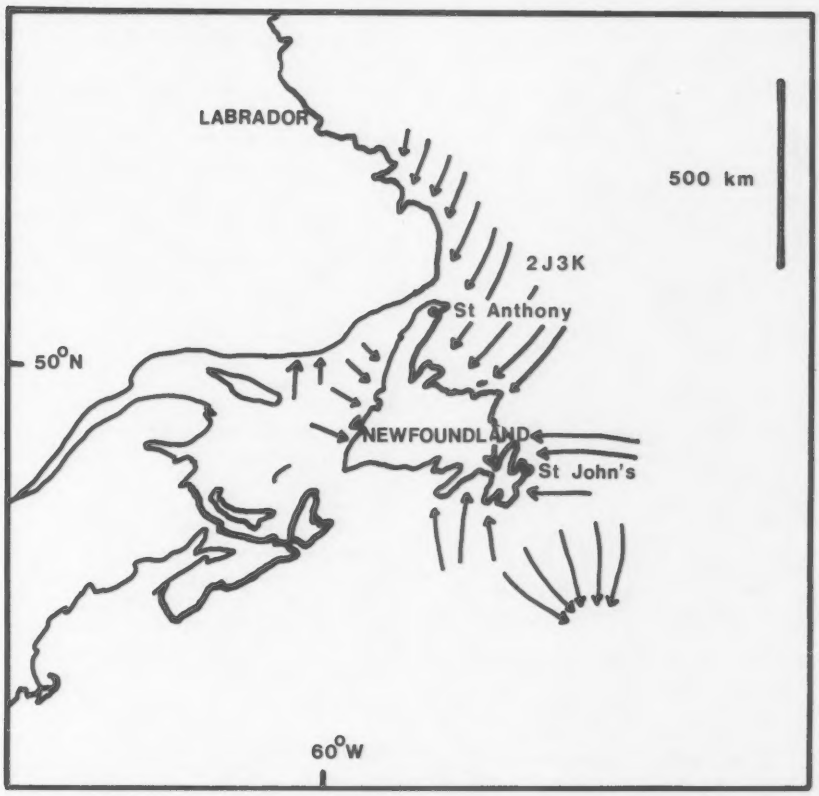

FIG. 1. Capelin stocks and spawning migrations in Newfoundland area, showing St John's and St Anthony, the endpoints of the northeast coast transects.

shoals during June and July. The larvae drift into deeper water, where the immature capelin feed before returning to shallow waters to spawn at 3–5 yr of age. Approximately 40% of 3-yr-old capelin, 50–70% of 4-yr-old capelin, and 93–100% of 5-yr-old capelin are mature, although these figures vary considerably with stock and year (Carscadden and Miller 1981; Carscadden et al. 1981). Very few capelin live beyond 5 yr of age.

Off Newfoundland, five major stocks of capelin (Fig. 1) have been identified (Carscadden 1983). Of these the stock northeast of Newfoundland and southern Labrador (NAFO areas 2J and 3K), which spawns along the northeast coast of Newfoundland and southern Labrador, appears to be the largest. The 2J3K stock also is represented by the longest time series of data, and since the stock area overlaps substantially with the location of the whale sightings used in this study, we chose it as an indicator of the status of the capelin stocks.

In this paper, the hypothesis that the abundance of whales inshore is related to capelin abundance was tested with correlation analysis using counts of whales along the northeast coast of Newfoundland and estimates of capelin year-class strength. The latter allowed a test of the relationship between whale abundance and the biomass of different ages of capelin. Predictive functions for whale abundance inshore were calculated, and used to investigate the probability of a return to the inshore humpback numbers of the late 1970s.

Methods

Between 1973 and 1983 (but excluding 1980) there have been a number of shipboard surveys of whales along the northeast coast of Newfoundland between St John's and St Anthony (Fig. 1). The route taken generally followed a path close to the shortest route between the two ports, although there was considerable variation. On each survey the observers included a professional and experienced cetologist. A count was made of the numbers of humpback, finback, and minke whales sighted on each survey (Table 1). A watch was kept for cetaceans throughout each survey, whatever the conditions. Sightings of whales made during halts or deviations from the survey route for the purposes of studying cetaceans were excluded from the counts. A variance-stabilizing square-root transformation was applied to both the counts and the mean counts over all surveys in any year.

Although the surveys between St John's and St Anthony were made from a variety of vessels (6-m sloop *Patience* to the large commercial ferry *William Carson*), at different times of year (15 July – 22 September), moving at various speeds, counts

TABLE 1. Mean annual counts of humpbacks, finback, and minke whales on surveys between St John's and St Anthony, with numbers of surveys for each year. Finback and minke counts were not available for one of the 1976 surveys.

Year	Number of surveys	Mean annual count		
		Humpbacks	Finbacks	Minkes
1973	1	0	13	3
1974	2	20	11	0.5
1975	1	17.5	11	1
1976	4	8.75	9.7	8.3
1977	2	54	9	10.5
1978	1	64	36	8
1979	1	111	20	5
1981	3	3	0.7	0.7
1982	1	10	0	10
1983	1	4	0	4
1984	1	0	1	3

within any year were reasonably consistent. There was significantly less variation between transformed humpback counts within a year than between years (F test, $P < 0.0005$). For finbacks and minkes, whose count showed less interyear variation, within-year and between-year variation did not differ significantly.

The transformed counts are compared with estimates of capelin year-class strength (as 2-yr-olds) from sequential cohort analysis of the 2J3K stock (Carscadden and Miller 1981) and predictions of year-class strength from abiotic variables from Leggett et al. (1983). (Similar predictions were obtained by Leggett et al. (1984), but because of a different statistical technique, slightly less efficient predictors were derived.) The capelin year-class strengths are logarithmically transformed, as in Leggett et al. (1983). For this analysis, it is assumed that the estimates of year-class strength of capelin at age 2 are indicative of relative year-class strengths for that cohort at all ages, even though natural mortality and spawning mortality undoubtedly vary annually. Different year-classes vary considerably, by over two orders of magnitude (e.g. Carscadden and Miller 1981), and an examination of available sampling data (J. E. Carscadden, unpubl. data) suggests that year-classes retain their relative strengths at all ages. Thus, it would appear that this assumption will not invalidate the analysis.

Results

Correlations between Whale Abundance and Capelin Year-Class

We calculated correlations between the northeast coast whale counts and the strengths of different aged year-classes (as estimated when 2 yr old) for capelin in the 2J3K stock (data as in Leggett et al. 1983). For instance, when comparing humpbacks and 3-yr-old capelin, the 1973 humpback count was compared with the strength of the 1970 year-class, the 1974 count with the 1971 year-class strength, etc. In Fig. 2 these correlations are shown plotted against capelin age for each whale species. The correlations present a fairly clear picture of the whales' responses to changing capelin year-class strengths.

The humpbacks appear to move offshore in response to strong year-classes of 3-yr-old capelin and to a lesser extent 2-yr-old capelin, but their inshore–offshore movement does not seem closely related to the abundance of 1- or 5-yr-old capelin. Figure 3 shows mean inshore humpback counts plotted against estimated 3-yr-old capelin biomass.

Finbacks also move offshore in response to high abundance of 2- to 3-yr-old capelin. There is an additional tendency for finbacks to move inshore when there are many 5-yr-old capelin. These 5-yr-old capelin are mature and will be spawning along the coast.

The minkes' response to varying year-class strengths presents a substantially different picture from that for humpbacks or finbacks. Minkes move offshore in response to high abundance of 1- to 2-yr-old capelin, but their distributions seem less related to the 3- to 5-yr-old year-classes.

Some caution must be exercised when attempting to derive biological relationships from correlation analysis. For instance, it is tempting to suggest that finbacks move inshore when abundance of young capelin is low. At the same time, the positive (though not significant) correlation between 5-yr-olds and finbacks suggests that the whales move inshore when this age-class is large. However, these events may be occurring at the same time; in any given year, when the abundance of finbacks inshore is high, it is possible that the abundance of immature capelin offshore is low, and mature 5-yr-olds is relatively high. To properly evaluate the possible biological relationships, a detailed multivariate analysis of many more years data would be necessary. However, the present correlation analysis does identify possible biological relationships which can be used to formulate hypotheses concerning species relationships.

Changing Whale Populations

Correlations between the northeast coast whale counts and year were calculated for each species in order to investigate whether there were significant overall increases or decreases in whale abundance over the period of the surveys. The only significant correlation was that for finbacks ($r = -0.635$, $P < 0.05$), whose numbers apparently decreased significantly between 1973 and 1983. This decline in finback abundance is borne out by a more comprehensive analysis of whale sightings over the entire Newfoundland area (Lynch and Whitehead 1984).

Predicting Whale Abundance

Unfortunately, there are no reliable direct estimates of capelin year-class strength after 1978, as this was the last year when there was a large enough fishery to obtain adequate samples for reliable assessment (Leggett et al. 1983). However, Leggett et al. (1983) have shown that capelin year-class strengths off Newfoundland can be predicted from a knowledge of mean spawning date and the abiotic variables WIND (a measure of the extent of unfavourable wind conditions during the period in which the larval capelin drift away from the spawning beaches) and TEMPSUM (a measure of seawater temperature during the months after spawning), taken from standard meteorological records. For the 2J3K stock their model has an r^2 of 0.73.

Stepwise multiple regressions of whale counts on year, and capelin year-class strength, as predicted by Leggett et al. (1983), were made. The results (Table 2) show that the estimated strengths of the 2- and 3-yr-old year-classes are excellent predictors of inshore humpback abundance. For finbacks the 3-yr-old year-class strength and year are also excellent pre-

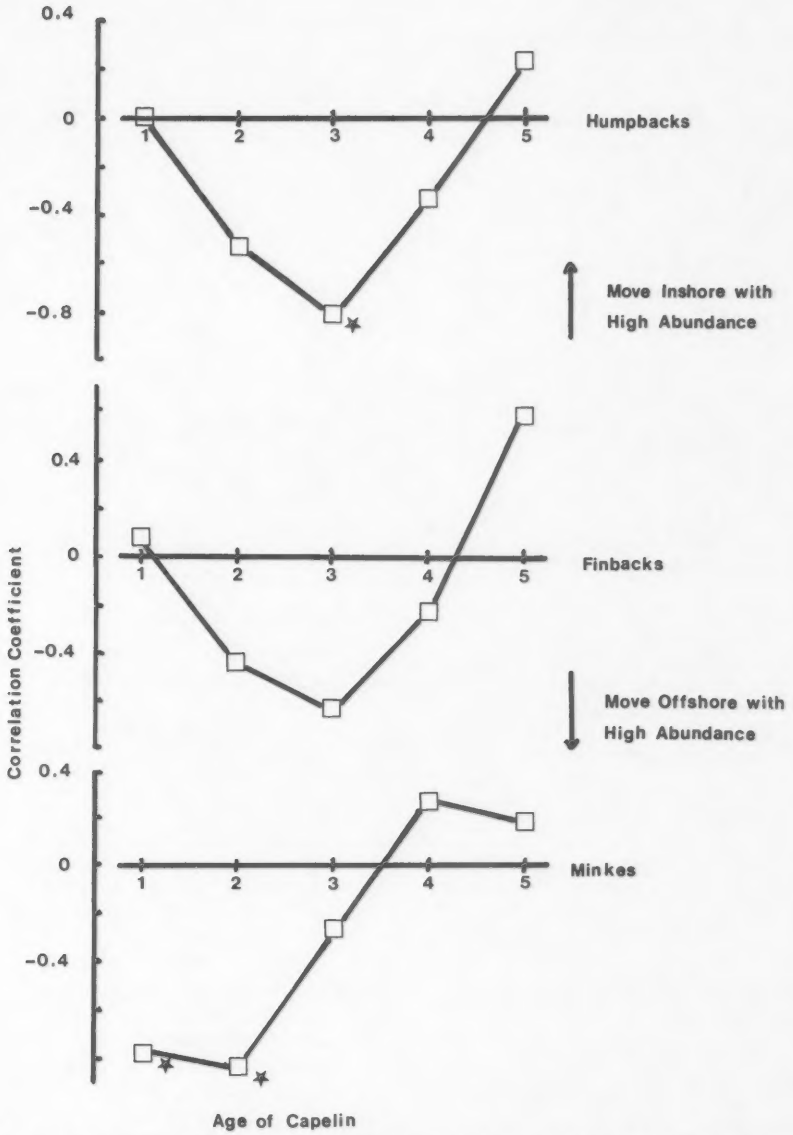

FIG. 2. Correlation coefficients between northeast coast whale counts and the strength of different aged year-classes of capelin in stock 2J3K. ★, correlations significant at $P < 0.05$.

dictors. Minke abundance is much less well predicted by these variables.

Thus, it seems that humpback and finback whale abundances on the northeast coast of Newfoundland can be predicted with reasonable accuracy, at least 1 yr in advance, using year-class strengths of capelin predicted from abiotic variables as in Leggett et al. (1983).

Extreme Years

The extreme abundance of humpback whales inshore during the late 1970s inflicted considerable hardship on the fishermen of Newfoundland. The regression given in Table 2 allows us to predict the probabilities of similar humpback densities occurring in the future. Assuming no correlation between adjacent capelin year-classes (there was no significant autocorrelation in the data presented by Leggett et al. (1983)), we calculated the probability of inshore abundances as large as, or larger than, those in the late 1970s (Table 3). If overall humpback and capelin populations do not change considerably, we can expect inshore humpback densities as high as, or higher than, in 1977 (54 humpbacks counted) once every 7 yr, in 1978 (64 humpbacks counted) once every 11 yr, and 1979 (111 humpbacks counted) once every 125 yr.

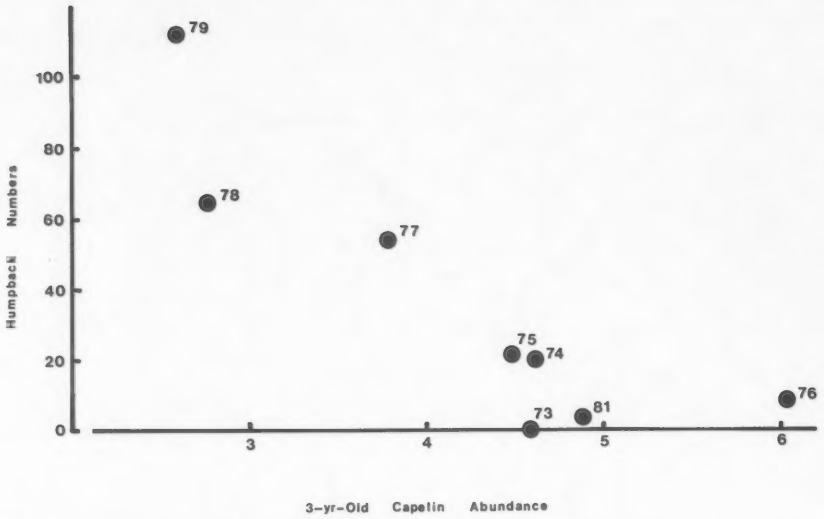

FIG. 3. Counts of humpback whales along the northeast coast of Newfoundland plotted against 3-yr-old capelin abundance in stock 2J3K (logarithmically transformed).

TABLE 2. Results of stepwise multiple regressions of northeast coast whale counts on year, and on estimated strength of year-class of different aged capelin from Leggett et al. (1983), for stock 2J3K. JK1 = 1-yr-old capelin in stock 2J3K, etc. The first three independent variables entered in each regression, their coefficients (after three variables had been entered), and values of r^2 at each step are given. Coefficients significantly different from zero: $*P < 0.05$; $**P < 0.01$. These regressions may be used to predict inshore whale abundance.

Dependent variable	Order entered in regression (coefficient/r^2)		
	1	2	3
Humpback	JK3 (−2.31**/0.61)	JK2 (−1.25*/0.80)	JK1 (0.92/0.88)
Finback	JK3 (−1.01**/0.46)	Year (−0.45**/0.79)	JK4 (−0.72/0.89)
Minke	JK2 (−0.71*/0.63)	Year (0.09/0.67)	JK1 (−0.24/0.73)

TABLE 3. Probabilities of counting more humpbacks along the northeast coast than in the extreme years of 1977, 1978, and 1979. Calculations use the regressions in Table 3, with the first two variables entered in the regression (2- and 3-yr-old capelin).

Year	Humpbacks counted	Probability that more humpbacks are counted
1977	54	0.14
1978	64	0.089
1979	111	0.008

Discussion

The predictors of humpback abundance inshore which have been obtained in this paper should be of considerable importance in the forecasting of entrapment damage to fishing gear in the short term. They will allow fishermen to be warned, at least 1 yr in advance, if severe entrapment problems are anticipated, and permit extensive whale release programs and other alleviating measures to be established.

This analysis also shows the range of variation in humpback abundance, and whale damage, that might be expected over the longer term (e.g. greater than 10 yr). This information is potentially valuable when deciding the general level of services, and the infrastructure, that are needed to deal with the whale entrapment problem. It also allows prediction of mean whale mortality from entrapment, important when considering the population dynamics of the whale stocks.

Extrapolations of these results over periods longer than 10 yr or so should be used cautiously: the absolute populations of the whales could change, and there might be significant variation in the general oceanography of the area which could in turn affect the population dynamics of both predators and prey. It is important that the oceanography, capelin abundance, and whale numbers continue to be monitored as systematically as possible.

What happened during the late 1970s when there was such a profusion of whales inshore? This analysis shows that the appearance of the whales was probably a natural consequence of changes in the status of the capelin stock. The late 1970s was a period of exceptionally low capelin abundance. This decline in the stock closely followed the development of the capelin fishery off Newfoundland during the mid-1970s. However, the fishery took only an apparently insignificant part of the available biomass, and Leggett et al. (1983) argued that the low

abundance was largely due to an unfavourable combination of environmental variables.

Whitehead and Lien (1982) have shown that the changes in whale abundance on different parts of the Newfoundland coast were not synchronous. While whale numbers at different locations along the northeast coast changed more or less in step, sighting and entrapment rates on both the south coast and off southern Labrador were out of phase with the northeast coast counts given in this paper. On the south coast, humpback sightings peaked in 1977, whereas off southern Labrador they increased during the early 1980s. A more fine-scale version of the analysis presented here might illuminate these variations, but there are not sufficient data on capelin on the south coast to describe the population dynamics of that stock. Additionally, humpback and finback whales make considerable migrations, crossing several NAFO areas during the summer (Mitchell 1974a; Whitehead et al. 1982). Thus, the presence of a whale inshore in a particular area might be a response to the lack of immature capelin in a stock which spawns in a different area. In this respect the 2J3K stock, the largest in the western North Atlantic, could have great significance in determining inshore whale distributions over the entire region.

For the humpbacks, at least, mature spawning capelin seem to be a secondary food source, generally used only when there are few immature capelin. This might be on account of the proximity to shore of the mature capelin, or some function of their schooling behaviour.

An interesting by-product of the analysis is the suggestion that minke whales may be generally eating younger capelin than humpbacks and finbacks. There has been some concern about possible trophic competition between baleen whale species off eastern Canada (Mitchell 1974b), and competition might be involved in the apparent recent decline in finback numbers (Lynch and Whitehead 1984). The kind of analysis performed here is one method of obtaining information on such competition.

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Comparison of Constant Effort Harvest Policies for Fish Stocks with Variable Recruitment

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Hightower, J. E., and G. D. Grossman. 1985. Comparison of constant effort harvest policies for fish stocks with variable recruitment. Can. J. Fish. Aquat. Sci. 42: 982–988.

Environmental variability may have a substantial influence on marine fish stocks, primarily by affecting survival to the time of recruitment. Simulation studies at low, intermediate, and high levels of variability in recruitment were used to compare alternative constant effort policies for anchovy (*Engraulis capensis*), Atlantic menhaden (*Brevoortia tyrannus*), and Pacific ocean perch (*Sebastes alutus*) fisheries. These policies were either to maintain effort at the level producing maximum sustainable yield (f_{MSY}), or to permit levels of effort 25–100% greater than f_{MSY}. An increase in effort of 25% above f_{MSY} typically did not reduce annual yield significantly; however, a significant reduction in yield was apparent in all cases when effort increased by 75–100%. When recruitment is highly variable, comparable yields may be obtained at several levels of fishing effort. In such cases, environmental variability provides the fishery manager with considerable flexibility to enhance social or economic benefits without decreasing yields significantly.

La variabilité environnementale peut avoir une influence importante sur les stocks de poissons marins, surtout pour la survie jusqu'à l'époque du recrutement. On a utilisé des études de simulation à des niveaux de variabilité du recrutement faible, intermédiaire et élevé pour comparer divers régimes d'effort constant pour la pêche de l'anchois (*Engraulis capensis*), de l'alose tyran (*Brevoortia tyrannus*) et du sébaste à longue mâchoire (*Sebastes alutus*). Ces régimes visaient soit le maintien de l'effort au niveau produisant un rendement maximal soutenu (f_{RMS}) ou un accroissement des niveaux d'effort le rendant de 25 à 100 % plus élevé que le f_{RMS}. Un effort supérieur de 25 % au f_{RMS} n'a pas abaissé le rendement annuel de façon significative ; toutefois, une baisse importante du rendement était évidente dans tous les cas quand l'effort était supérieur de 75 à 100 %. Quand le recrutement est très variable, on peut obtenir des rendements comparables à plusieurs niveaux d'effort de pêche. Dans de tels cas, la variabilité environnementale procure une grande latitude au gestionnaire des pêches pour accroître les avantages sociaux ou économiques sans abaisser nettement les rendements.

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Management plans for the regulation of commercial fisheries usually restrict either fishing effort or catch. Catch quotas have received greater use historically (Sissenwine and Kirkley 1982); however, imposition of a catch quota may lead to stock depletion after several years of poor recruitment (Swartzman et al. 1983). In addition, desired fishing mortality rates are achieved more directly by regulation of fishing effort than by catch restrictions (Sissenwine and Kirkley 1982). For these reasons, this study is based on a comparison of management plans in which harvests are regulated through restrictions on fishing effort.

Development of an effective management plan is difficult because environmental factors may have a substantial influence on fish stocks, primarily by affecting survival to the time of recruitment (Getz and Swartzman 1981). A direct effect of this variability in year-class strength is variability in annual catch (Gulland 1972, 1982; Hennemuth et al. 1980), and a fishery may be supported for several years largely by a single strong year-class. An indirect effect of this phenomenon is that, because stock size is not constant, the optimal level of fishing effort also varies. This suggests that similar harvests may be obtained at a range of effort levels; therefore, moderate errors in estimating the optimal level of fishing effort would be acceptable. In addition, flexibility in selecting effort regulations might enable the fishery manager to enhance social or economic benefits without decreasing yields significantly.

Simulation studies have been useful in evaluating alternative fishery management plans. For example, Huang and Walters (1983) compared alternative strategies for rehabilitation of a large yellow croaker (*Pseudosciaena crocea*) stock and Archibald et al. (1983) estimated steady-state yields obtained from a Pacific ocean perch (*Sebastes alutus*) stock at different levels of fishing effort. In both studies, variability in recruitment was simulated by incorporating an error term into the stock–recruitment relationship (SRR). Simulation studies might also be used to compare frequency distributions of annual harvest obtained at different levels of fishing effort. This comparison may be informative because, even though steady-state or expected yield differs at different levels of fishing effort, such differences may not be of practical importance.

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Consider, for example, regulation of a fishery in which the stock is moderately overexploited and alternative employment is not available. In this case, expected yield will be increased by imposition of a theoretically optimal management plan (optimal in the sense that yield is maximized). The management plan also may have substantial socioeconomic impacts because maximum sustainable yield (MSY) is obtained by decreasing fishing effort, and these impacts could be unacceptable if observed yields did not increase noticably. The success of any MSY policy depends not only on the accuracy of supporting biological data and compliance within the fishery, but also on the unpredictable effect of the environment on recruitment. By incorporating an appropriate error term into the SRR, age-structured models can be used to predict whether observed changes in yield brought about by decreasing effort will be worth the accompanying socioeconomic disruption.

In this study, we examined published data on stock size and recruitment to determine typical levels of variability in recruitment. Simulation studies at low, intermediate, and high levels of variability were used to compare alternative management policies for anchovy (*Engraulis capensis*), Atlantic menhaden (*Brevoortia tyrannus*), and Pacific ocean perch fisheries. Using maximization of yield as a management goal, these comparisons were done to predict changes in yield that result from changes in fishing effort for fish of varying life spans at three levels of environmental variability.

Methods

The Stock–Recruitment Relationship

Several models of varying complexity have been proposed to examine the relationship between parental stock and recruitment (Beverton and Holt 1957; Cushing 1971; Larkin 1973; Ricker 1975; Getz and Swartzman 1981; Shepherd 1982). Minimum features required for a biologically realistic SRR are (1) low recruitment at very low stock sizes and (2) the ability to allow recruitment to vary widely at intermediate stock sizes (Shepherd 1982; Swartzman et al. 1983; Strong 1984). The Ricker and Beverton–Holt stock–recruitment models are most commonly used to model fish populations, and both models predict lower recruitment as stock size approaches zero. To introduce an appropriate level of environmental variability into the SRR, it is first necessary to determine what form this term should take.

A multiplicative lognormal error term has been used in recent studies of stock–recruitment models (Allen 1973; Walters and Hilborn 1976; Peterman et al. 1978; Laurec et al. 1980; Peterman 1981; Walters and Ludwig 1981; Archibald et al. 1983; Huang and Walters 1983) of the general form

$$R = f(S)e^{v}$$

where R = recruitment, $f(S)$ = some function of parental stock, which is often represented by biomass of spawners (Beverton 1962; Doubleday 1976; Deriso 1980; Shepherd 1982), and v = normally distributed random variate with mean 0 and variance σ^2.

This multiplicative lognormal error term has been used in studies of salmon populations, both for mathematical convenience as well as for assumed biological realism (Peterman 1981). A theoretical justification for use of this error term is that e^{v} can be viewed as a random survival factor resulting from several independent and multiplicative environmental factors (Walters and Hilborn 1976). Thus, v represents the sum of several random factors and should be approximately normally distributed by the Central Limit Theorem (Walters and Hilborn 1976). The lognormal error distribution is biologically appealing because it provides a simple representation of the observed effects of environmental variability (i.e. good environmental conditions can produce very large year-classes, while poor environmental conditions can reduce recruitment to zero at most). In addition, increased variability in recruitment would seem more likely when the spawning stock is large (Gulland 1967), and use of a multiplicative error term assumes that variability will increase as stock size increases. The lognormal distribution also more accurately represents the frequency distribution of observed year-class strength (Hennemuth et al. 1980) and salmonid survival rates (Peterman 1981) than the normal distribution.

In this paper, we assume that a lognormal error term is appropriate and estimate the magnitude of the lognormal error variance for 13 multi-aged marine fish stocks (Table 1). Minimum criteria for inclusion of a data set were as follows: (1) at least 10 yr of data were available, (2) parental stock was estimated either as stock biomass, biomass of spawners, or a measure of egg production, and (3) recruitment was given as numbers of fish.

Three models were fitted to each data set for the following reasons. For a particular stock, model selection may be based on biological information (Nelson et al. 1977); however, alternative models can rarely be excluded using statistical tests (Gulland 1967). Second, because a regression estimate of the residual error variance includes both the true random error and a lack-of-fit component, we used three possible models to evaluate the sensitivity of our estimates to the form of the model:

$$(1)\quad R = \mu e^{v}$$

$$(2)\quad R = \alpha S e^{-\beta S} e^{v}$$

$$(3)\quad R = 1/(\gamma + \delta/S)e^{v}$$

where μ, α, β, γ, and δ are parameters. The first model assumes that no relationship exists between stock size (S) and recruitment (R). The second is the Ricker model (Ricker 1975) and the third is that of Beverton and Holt (Ricker 1975). A constant recruitment model was included to evaluate the increase in error variance which results from the use of a simpler (and conceptually different) model, although the model violates the above criterion that recruitment should decrease at very low stock sizes.

Because the log-transformed Ricker model is a linear equation and has an additive error term, the residual error variance (σ^2) was estimated using linear regression. The Beverton–Holt model was fitted with nonlinear regression as $\ln(R) = \ln(1/(\gamma + \delta/S)) + v$ to obtain an estimate of σ^2. Initial parameter estimates for the Beverton–Holt model were obtained by transforming the model to use linear least-squares regression (Ricker 1975), and these estimates were used as starting values for nonlinear regression analysis. Bounded nonlinear regression (SAS Institute, Inc. 1982) was required to obtain reasonable parameter estimates ($\delta > 0$) for one stock, the North Sea plaice; Ricker (1975) also noted this problem when fitting a Beverton–Holt curve to these data using linear regression.

Parameterization of Age-Structured Model

To explore the relationship between number of age classes (λ) and response to overexploitation, parameter estimates were

TABLE 1. Description of the 13 fish stocks used to estimate the level of random variability in the stock–recruitment relationship. The number of observations in each data set is given as N.

Common name	Scientific name	Area	N	Source[a]
Herring	*Clupea harengus*	Norwegian[b]	20	A
		Georges Bank	13	B
		Icelandic[b]	23	C
		Icelandic[c]	29	C
Round herring	*Etrumeus teres*	South Africa	13	D
Sardine	*Sardinops caerulea*	California	33	E
Atlantic menhaden	*Brevoortia tyrannus*	Atlantic	16	F
Pacific halibut	*Hippoglossus stenolepis*	Pacific	46	G
Plaice	*Pleuronectes platessa*	North Sea	26	H
Pilchard	*Sardinops ocellata*	South Africa	26	D
Anchovy	*Engraulis capensis*	South Africa	13	D
Atlantic mackerel	*Scomber scombrus*	Northwest Atlantic	16	I
Large yellow croaker	*Pseudosciaena crocea*	China Sea	22	J

[a]Source: A, Dragesund et al. 1980; B, Anthony and Waring 1980; C, Jakobsson 1980; D, Newman and Crawford 1980; E, Troadec et al. 1980; F, Nelson et al. 1977; G, Deriso and Quinn 1983; H, Ricker 1975; I, Anderson and Paciorkowski 1980; J, Huang and Walters 1983.
[b]Spring-spawning.
[c]Summer-spawning.

TABLE 2. Parameter estimates for the age-structured model of anchovy stock dynamics (from Getz 1985). Number of age-classes (excluding age 0): $\lambda = 5$; length of harvesting season: $t' = 0.67$ yr; stock–recruitment model: Beverton–Holt (spawning after harvesting season), parameter estimates: $\hat{\gamma} = 0.0082$, $\hat{\delta} = 0.9016$; lognormal error variance: $s^2 = 0.06$[a]; range of effort levels (arbitrary multipliers) used in simulations: $f = 0$–4.

Age	Weight (g)	Fecundity index (g)[b]	Catchability (normalized)	Natural mortality
1	1.6	0.8	0.24	0.8
2	6.9	6.9	0.36	0.8
3	14.0	14.0	0.42	0.8
4	19.0	19.0	1.00	0.8
5	24.0	24.0	1.00	0.8

[a]An estimate of the lognormal error variance was obtained from total stock biomass and recruitment estimates from 1964 to 1976 (Newman and Crawford 1980). Getz (1980) obtained parameter estimates for the Beverton–Holt SRR using estimates of spawning stock biomass and recruitment from 1964 to 1978 but did not publish the stock–recruitment data.
[b]Average weight multiplied by the proportion that are fecund.

obtained for a relatively short-lived anchovy stock ($\lambda = 5$) from the west coast of South Africa (Table 2; from Getz 1985) and for a relatively long-lived stock of Pacific ocean perch ($\lambda = 29$) (Table 3; from Archibald et al. 1983). Note that λ represents the maximum age-class used in the model, and not the life span of the fish. Recent aging studies using sectioned otoliths indicate that Pacific ocean perch may live for more than 70 yr (Archibald et al. 1981). Data used in this simulation study were obtained through stock reconstruction (Archibald et al. 1983), using catch-at-age data obtained by surface readings of otoliths. Sufficient data are not yet available from aging otolith sections to permit reanalysis. Parameter estimates for Atlantic menhaden, a fish of intermediate life span ($\lambda = 8$), were obtained primarily from life history studies and previous analyses of catch and effort data (Table 4). (In-depth analyses of the Atlantic menhaden fishery are given by Schaaf and Huntsman (1972), Schaaf (1975), Nelson et al. (1977), and Schaaf (1979).) Numbers-at-age were obtained from cohort analysis (Pope 1972) using catch-at-age and fishing effort data (Schaaf 1979) and estimates of mean instantaneous natural mortality rate ($M = 0.25$) and mean catchability (Vaughan 1977). As in earlier studies of Atlantic menhaden stock dynamics (Schaaf and Huntsman 1972; Nelson et al. 1977; Schaaf 1979), the Ricker curve was used to represent the SRR. Spawning potential was represented by the estimated biomass of spawning females, and was obtained as

$$\sum_{i=1}^{\lambda} c_i N_{it}$$

where N_{it} is the number of age-i fish in year t and c_i, the fecundity parameter for age-i fish, is defined as

$$c_i = s_i f_i w_i$$

where s_i = proportion of females that are sexually mature at age i (Vaughan 1977), f_i = proportion of age i fish that are females (Reintjes 1969), and w_i = weight of females at age $i + 0.5$ from a von Bertalanffy growth curve (Reintjes 1969).

Estimates of weight-at-age were obtained by using sex-specific von Bertalanffy curves (Reintjes 1969) to predict mean weight at ages 1.5–8.5. A von Bertalanffy curve was fitted to data for both sexes and used to predict overall mean weight-at-age.

Evaluation of Alternative Constant Effort Policies

Once typical levels of variability in recruitment were determined, it was possible to evaluate the effects of this variability on alternative constant effort policies. This was done by incorporating a lognormal error term into an age-structured model containing a SRR; a complete description of such a model is given by Archibald et al. (1983) or Huang and Walters (1983).

To estimate MSY for each stock, estimates of steady-state average yield were obtained at each level of fishing mortality using the following replication–deletion approach (Law and Kelton 1982). Each of 100 replicates was run for 10λ yr, and average annual yield was obtained for the last 5λ yr. Observations from the first 5λ yr were deleted to reduce the influence of the nominal set of initial conditions.

TABLE 3. Parameter estimates for the age-structured model of Pacific ocean perch stock dynamics (from Archibald et al. 1983). Recruitment occurs at age 6, so weight, catchability, and natural mortality are set to 0 for ages 1–5. Number of age-classes (excluding age 0): $\lambda = 29$; length of harvesting season: $t' = 1.00$ yr; stock–recruitment model: Ricker (spawning at start of year), parameter estimates: $\hat{\alpha} = 0.0883$, $\hat{\beta} = 9.01 \times 10^{-5}$; lognormal error variance: $s^2 = 0.30$; range of effort levels (arbitrary multipliers) used in simulations: $f = 0.0$–0.40.

Age	Weight (10^{-2} kg)	Fecundity index	Fishing mortality[a]	Natural mortality
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0
5	0	0	0	0
6	0.00485	0	0.010	0.05
7	0.00529	0	0.021	0.05
8	0.00572	0	0.040	0.05
9	0.00614	0	0.069	0.05
10	0.00654	0	0.111	0.05
11	0.00694	1.00	0.162	0.05
12	0.00732	1.22	0.217	0.05
13	0.00770	1.47	0.266	0.05
14	0.00806	1.72	0.297	0.05
15	0.00841	1.97	0.304	0.05
16	0.00876	2.20	0.284	0.05
17	0.00909	2.44	0.243	0.05
18	0.00942	2.67	0.190	0.05
19	0.00973	2.92	0.190	0.05
20	0.01000	3.11	0.190	0.05
21	0.01030	3.31	0.190	0.05
22	0.01060	3.48	0.190	0.05
23	0.01090	3.65	0.190	0.05
24	0.01120	3.83	0.190	0.05
25	0.01150	3.83	0.190	0.05
26	0.01170	3.83	0.190	0.05
27	0.01200	3.83	0.190	0.05
28	0.01220	3.83	0.190	0.05
29+	0.01300	3.83	0.190	0.05

[a]B. M. Leaman, Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C., pers. comm. These estimates of fishing mortality at age in 1977 were obtained through stock reconstruction (Archibald et al. 1983) and were multiplied by arbitrary constants (termed effort) to produce desired levels of fishing mortality.

Once MSY and the associated level of fishing effort (f_{MSY}) were estimated, simulation studies were used to compare the MSY effort policy with constant effort policies where effort was 25, 50, 75, and 100% greater than f_{MSY}. Each treatment combination represented one of three levels of variability in recruitment, one of three fish stocks, and one of four pairwise comparisons of f_{MSY} versus an alternative effort level. The starting age distribution for each simulated period of $k = 5\lambda$ yr was obtained from a deterministic version of the model (Getz 1980), using the level of effort that produced MSY for the deterministic model.

Because the commercial fisherman is affected by annual changes in recruitment and subsequent fluctuations in harvest, we emphasized annual harvest rather than mean or total harvest. However, consecutive harvests in each k-yr period are not independent, and harvests in the first few years are affected by the starting conditions. To obtain independent replicates that are less biased by initial conditions and therefore better estimates of steady-state responses, we analyzed only the harvest from year k in each k-yr period. Harvests in years 1 through $k - 1$ also would be of interest to the fisherman and fishery manager. However, these harvests would tend to be more similar among treatments than harvests in year k due to the shared starting conditions. By focusing the analysis on the steady-state behavior of the system, we obtain conservative results about the similarity in performance of alternative policies. One hundred replicates were used for each treatment. Note that the sample size is arbitrary and that our ability to detect differences among treatments would increase with an increase in sample size. We contend that a difference of practical significance should be detectable by observing 100 independent trials, and note that only a single trial would be observed after implementation of a management plan. Differences in the frequency distribution of harvest in year k were tested at the 95% confidence level using a two-tailed Kolmogorov–Smirnov test (Siegel 1956).

TABLE 4. Parameter estimates for the age-structured model of Atlantic menhaden stock dynamics. Number of age-classes (excluding age 0): $\lambda = 8$; length of harvesting season: $t' = 1.00$ yr; stock–recruitment model: Ricker (spawning at start of year), parameter estimates: $\hat{\alpha} = 0.0205$, $\hat{\beta} = 0.0024$; lognormal error variance: $s^2 = 0.25$; range of effort levels (vessel-weeks) used in simulations: $f = 0$–1000.[a]

Age	Weight (g)	Fecundity index (g)	Catchability[b]	Natural mortality
1	102.77	0	0.000577	0.25
2	260.21	110.25	0.001805	0.25
3	411.73	227.37	0.001579	0.25
4	530.31	302.70	0.001540	0.25
5	614.28	354.63	0.001430	0.25
6	670.60	410.44	0.001820	0.25
7	707.23	491.98	0.001703	0.25
8	730.63	496.60	0.001703	0.25

[a]Estimates of annual effective fishing effort (adjusted for changes in catchability using 1971 as the base year) are given by Schaaf (1979). The range 0–1000 vessel-weeks includes most observed values and all published estimates of the level of fishing effort that produces MSY.

[b]Age-specific catchability estimates were obtained from cohort analysis. Effective fishing effort data (Schaaf 1979) and an estimate of mean catchability (Vaughan 1977) were used to obtain starting values for fishing mortality rates.

Results and Discussion

Few of these stocks displayed evidence of a relationship between stock size and recruitment, and neither the Ricker nor Beverton–Holt curve appeared to account for a significant amount of variation in recruitment. Estimates of σ^2 (s^2) ranged from 0.06 to 1.20 for both the Ricker and Beverton–Holt models. Under the assumption that no relationship exists between stock size and recruitment, s^2 ranged from 0.07 to 5.68. The distribution of s^2 was similar for the three models (Fig. 1), and in all but two cases (California sardine and Icelandic spring-spawning herring), s^2 does not increase substantially when no relationship between stock size and recruitment is assumed. For the three models considered, most values were less than 0.75, and three values were selected arbitrarily to represent low (0.25), moderate (0.50), and high (0.75) levels of

TABLE 5. Comparison of annual yields obtained at the level of fishing effort that produced maximum sustainable yield (f_{MSY}) with yields obtained when effort exceeded f_{MSY} by 25, 50, 75, or 100%. For each paired comparison, frequency distributions of annual yield were compared using a Kolmogorov–Smirnov test ($\alpha = 0.05$), and significant differences are denoted by the letter *Y*. Estimates of the percentage increase in variability in steady-state average yield are given in parentheses as $100 \times (CV_i - CV_{MSY})/CV_{MSY}$, where CV_{MSY} and CV_i represent coefficients of variation when effort equals f_{MSY} or exceeds f_{MSY} by i = 25, 50, 75, or 100%. Three values of the lognormal error variance (σ^2) were used to represent levels of environmental variability in the period following implementation of a management plan.

	Increase in effort above f_{MSY} (%)											
	$\sigma^2 = 0.25$				$\sigma^2 = 0.50$				$\sigma^2 = 0.75$			
	25	50	75	100	25	50	75	100	25	50	75	100
Anchovy	*N* (−13)	*N* (24)	*Y* (45)	*Y* (72)	*N* (24)	*N* (23)	*Y* (48)	*Y* (50)	*N* (0)	*N* (38)	*Y* (31)	*Y* (44)
Menhaden	*N* (10)	*Y* (45)	*Y* (109)	*Y* (118)	*N* (27)	*Y* (60)	*Y* (43)	*Y* (106)	*N* (22)	*N* (13)	*Y* (60)	*Y* (113)
Perch	*Y* (57)	*Y* (13)	*Y* (114)	*Y* (138)	*N* (18)	*N* (36)	*Y* (64)	*Y* (120)	*N* (15)	*N* (31)	*Y* (90)	*Y* (164)

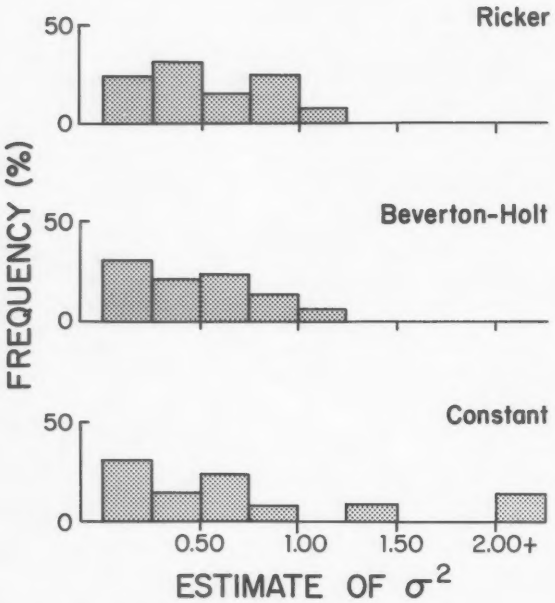


FIG. 1. Sample distribution of s^2, the error variance of the stock–recruitment relationship, for 13 multi-aged fish stocks. Ricker, Beverton–Holt, and constant recruitment models were fitted to each data set and a multiplicative lognormal error term was assumed.

variability for a general evaluation of the effect of variability in recruitment on alternative management scenarios.

For the simulated anchovy fishery, changes in the level of environmental variability had no detectable impact on comparisons of alternative policies (Table 5). For the Atlantic menhaden and Pacific ocean perch fisheries, increases in environmental variability obscured differences in yield obtained at different levels of fishing effort.

An increase in effort of 25% above f_{MSY} typically did not decrease yield significantly (Fig. 2; Table 5). Significantly lower yields were obtained in all cases when effort increased by 75–100% above f_{MSY}. It should be noted that the Kolmogorov–Smirnov test is sensitive to differences in location or dispersion (Siegel 1956); hence, significant differences may be due in part to increased variability in yield associated with increased fishing effort (Table 5). These results suggest that, even if future levels of environmental variability are relatively high, reductions in effort for heavily fished stocks should provide higher and less variable annual yields. When differences between current effort and f_{MSY} are less than 25–50% of f_{MSY}, changes in the magnitude or variability of annual yield may be insufficient to justify implementation of an MSY policy.

The approach demonstrated here can be used to contrast the effectiveness of any alternative policies that require different levels of fishing effort. Alternative policies might arise from different management models, from using different parameter estimates for a single model, or from a comparison of theoretically optimal and current levels of effort. The theoretically optimal or target level of effort need not be f_{MSY}. For example, Doubleday (1976) noted that when effort is reduced below f_{MSY}, losses in average yield may be offset by increases in catch per unit effort or reductions in the variability of yield. Selection of a target level of effort or index of policy performance is dependent on the fishery manager's objectives. In this study, yield maximization was assumed to be the management objective, and we evaluated changes in the distribution of annual harvest. However, changes in the distribution of catch per unit effort or net income may be equally important outcomes of a change in the level of fishing effort. Finally, stochastic models also can be used for risk analysis; for example, they can be used to estimate the probability that stock biomass will fall below an arbitrary level (Getz and Swartzman 1981; Archibald et al. 1983).

Further evidence that yield may be comparable at several levels of fishing effort was provided by Getz and Swartzman (1981). They developed a probabilistic age-structured model that was used to estimate variability in sustained yield at a range of levels of fishing effort. Results from their study indicate that, when recruitment is highly variable, significant differences in yield may be difficult to detect unless changes in the level of fishing effort are substantial. Thus, environmental variability, which produces these fluctuations in recruitment, might be viewed as advantageous in that it provides the fishery manager with considerable flexibility to incorporate socioeconomic

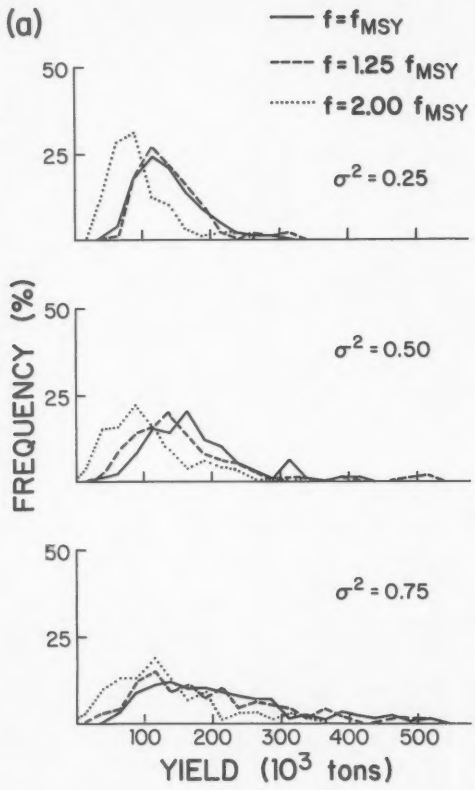
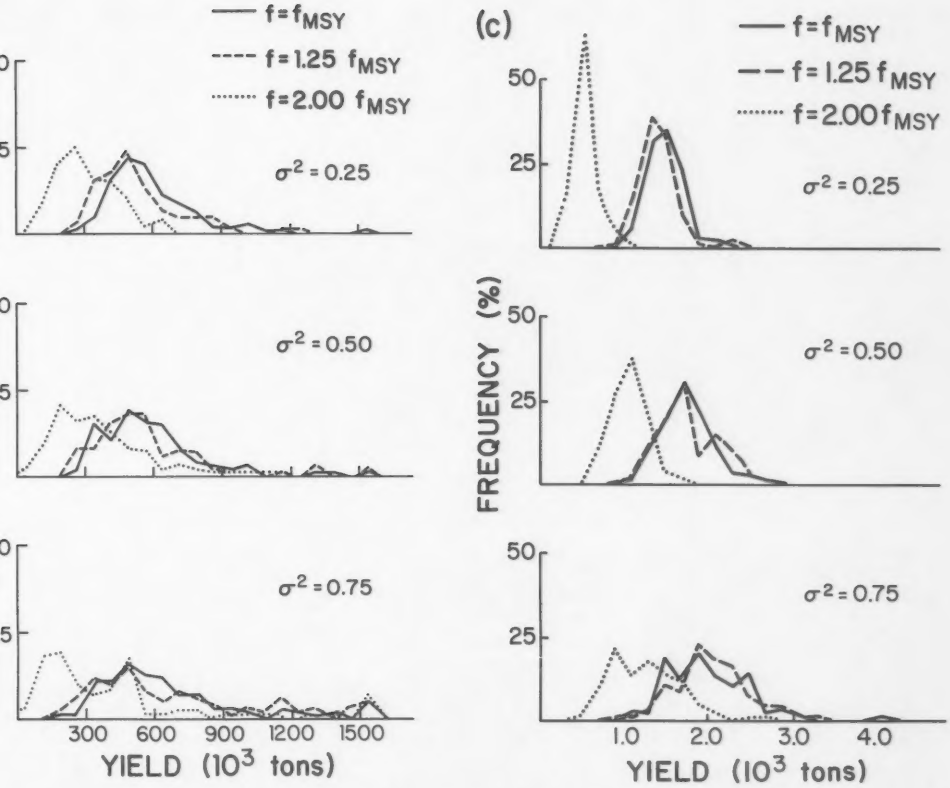


FIG. 2. Frequency distributions of harvest for (a) anchovy, (b) Atlantic menhad yield (f_{MSY}) or levels 25 and 100% greater than f_{MSY}. For each treatment combin variability in the stock–recruitment relationship is given as σ^2.



menhaden, and (c) Pacific ocean perch obtained by maintaining effort at the level that produces maximum sustainable combination, one of four frequency distributions of harvest at f_{MSY} was randomly selected for plotting. Environmental

factors into a management plan. Because these factors can rarely be ignored in policy formulation (Schoning 1984), it is encouraging to know that fishing effort may differ from a theoretically optimal level without resulting in a detectable reduction in harvest.

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Interaction Between Stock Area, Stock Abundance, and Catchability Coefficient

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The relationship between commercial catch-rates and population density upon which many stock assessment models depend assumes that stock area (A) is constant and independent of population abundance. Starting from a theoretical demonstration that the catchability coefficient (q) is inversely proportional to A, we establish the empirical basis of this relationship through comparisons of q and A of various Northwest Atlantic herring (*Clupea harengus harengus*) stocks and, in more detail, for Fortune Bay herring. For these stocks the relationship was of the form $q = cA^{-b}$. For Atlantic herring stocks, levels of b were in excess of 0.80. In Fortune Bay herring, reductions in abundance were accompanied by proportional reductions in A, which in turn was inversely correlated with changes in q. School size, measured as catch per set, also declined as population levels declined but the change was not proportional. Published findings indicate that pelagic stocks in particular, and fish stocks in general, exhibit a common response of reductions in A with interactive increases in the q during periods of rapid population decline. We conclude that the conventional assumption of a constant stock area is usually violated due to the systematic interaction between A and population abundance which is reflected in an inverse relationship between stock abundance and q. Calibration of sequential population models should therefore be restricted to research vessel data collected in a standard manner and covering the distributional area of the stock.

Pour la relation entre les taux de capture commerciale et la densité des populations dont dépendent de nombreux modèles d'évaluation des stocks, on suppose que la zone du stock (A) est constante et indépendante de l'importance numérique d'une population. La preuve théorique que le coefficient de capturabilité (q) est inversement proportionnel à A sert à établir la base empirique de cette relation à l'aide de comparaisons de q et de A chez divers stocks de hareng (*Clupea harengus harengus*) de l'Atlantique nord-ouest et, en plus grand détail, chez le hareng de la baie Fortune. Pour ces stocks, la relation prenait la forme $q = cA^{-b}$ et chez les stocks de hareng de l'Atlantique, b était supérieur à 0,80. Pour le hareng de la baie Fortune, une baisse du nombre s'accompagnait de réductions proportionnelles de A qui était en corrélation inverse avec les variations de q. La taille des bancs, quantifiée par les prises / mouillage, a aussi baissé en fonction d'un déclin de la population mais cette variation n'était pas proportionnelle. Les données publiées révèlent que les stocks pélagiques, en particulier, et les stocks de poissons, en général, montrent une réaction commune aux baisses de A et des accroissements interactifs de q pendant les périodes de baisse démographique rapide. Les auteurs formulent la conclusion que l'hypothèse classique d'une zone du stock constante est habituellement faussée à cause d'une interaction systématique entre A et l'importance numérique d'une population, interaction généralement traduite par une relation inverse entre l'importance numérique d'un stock et q. L'étalonnage des modèles démographiques séquentiels devrait donc être restreint aux données recueillies de façon normalisée par des navires de recherche dans la zone de répartition du stock.

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The relationship between indices of fishing effort, catch-rate, and fish abundance is of critical importance to the effective management of commercial fisheries, particularly with the increasing use of catch quotas as a means of optimizing yield. Such quotas place high demands on the timeliness and accuracy of scientific advice, which in turn requires detail and precision in the assessments of stock status and the impact of fishing on the resource. A perusal of the scientific reports of such fisheries commissions as NAFO and ICES indicates a continued heavy dependence of stock assessments on commercial catch and effort data, mainly as a source of calibration of sequential population models. This persistent reliance on commercial catch-rate data is surprising given the extensive literature (e.g. Paloheimo and Dickie 1964; MacCall 1976; Clark and Mangel 1979; Pope 1980; Ulltang 1980) on the failure of the underlying assumption of a constant catchability coefficient (q) (Beverton and Holt 1957) which underpins the classic catch equation of Baranov (1918). Garrod (1964) and Gulland (1964) have pointed out that variations in q may result from any number of factors including changes in fishing power, vulnerability to the gear, seasonal and spatial patterns of distribution, and changes in stock abundance. Some of these factors can be readily measured and taken into account to provide standardized catch-rates such as those derived by the multiplicative model of Gavaris (1980). However, other factors such as those inherently related to changes in abundance are

more difficult to assess, since they require a long time-series of independent estimates of abundance. In this paper we demonstrate that there is an additional property of the catchability coefficient relating to stock area which is fundamental to the proper interpretation of commercial catch-rate data. The theoretical basis of this property is presented and an instructive example is described. The degree of adherence of empirical results to theory allows us to evaluate the acceptability of commercial catch data as unbiassed estimates of population density.

Theoretical Basis

The catch of a particular gear per unit of its operation (c/f) is a product of the number of fish (n) present in the area swept by the gear times the elemental efficiency (Paloheimo and Dickie 1964) of that gear (p), i.e.

(1) $c/f = pn.$

In the context of this single unit of effort, p is the proportion of fish in the swept area that will be caught. Extension of relationship (1) to the entire populaton (N) for combined catches from a number of localities and over a period of time (C/F) requires an estimate of the fishing power of the gear, i.e. the proportion of the total area (A) occupied by the stock that is covered by a single sweep of the gear (a). Thus, we have

(2) $$C/F = \frac{paN}{A}$$

whence,

(3) $$\frac{C/F}{N} = \frac{pa}{A}$$

from which we define

(4) $$q = \frac{pa}{A}.$$

This proportionality constant, q, is equivalent to the catchability coefficient as defined by Holt et al. (1959) and is in effect the probability of capturing a fish in a single unit of effort. As noted by Paloheimo and Dickie (1964) the catchability coefficient is inversely proportional to the area, A, occupied by the stock. However, the corollary of the inverse relationship between q and A has received little attention in the published literature; it implies that a unit of effort will generate not only a higher fishing mortality rate but also a higher catch-rate in a small area as compared with a larger area for the same size of stock. Since stock area is difficult to measure, it is the common practice among fisheries biologists to assume that this parameter remains constant and independent of changes in population abundance. We now attempt to demonstrate that this assumption is often violated due to the systematic interaction between stock area and population abundance which tends to be reflected in an inverse relationship between stock abundance and q.

An Empirical Test

Expressions (3) and (4) demonstrated that q is inversely proportional to both stock area, A, and population size, N. If the systematic interaction between N and A is linear then the relationship between q and A will be adequately described by expression (4). However, the rate of population expansion and retreat within the general stock range is unlikely to be uniform, since habitat conditions will be less favourable at the extremes of the range than at its centre. Blaxter and Holliday (1963) have concluded, for example, that stock movements will occur more rapidly in areas of unfavourable habitat. In this case the interaction between N and A will be nonlinear. We posit, therefore, that the relationship between q (defined as the ratio of catch-rate to biomass) and A will take the form

(5) $q = cA^{-b}$

where $c = pa$ is a constant and b is a coefficient that describes the rate at which q will systematically vary with stock area; i.e. q will only be constant in the special case when $b = 0$. A value of $b = 1$ will indicate that changes in stock area have occurred in direct proportion to changes in stock abundance. In general, the larger the value of b the greater the distortion it will introduce into the catch-rate index. We have chosen as our standard vessel class the large purse-seine fleet which exploited nearly all of the herring populations in Atlantic Canada during the late 1960's and 1970's. The effort standard refers to operating time (which includes both searching and fishing time), and stock areas have been defined according to boundaries established by their respective NAFO or Canadian Statistical Areas and are consistent with stock assessment definitions of stock areas. For the special case of Bay of Fundy (4VWX) herring which belong to the "oceanic" complex of herring (Anthony and Waring 1980), the seaward stock boundaries have been defined by the 200-fathom (300-m) depth contour. The period chosen for comparison reflects the need for insensitivity of sequential population estimates of biomass to input parameters and a common time period to account for any technological changes within the constraints of data availability. The stock areas are shown in Fig. 1 and relevant data are summarized in Table 1. From Fig. 2, we can confirm that the catchability coefficient of the large purse-seine fleet is inversely proportional, in nonlinear fashion, to stock area and is of the form described by relationship (5).

It may be argued that the inverse relationship between catchability coefficient and stock area is peculiar to such active encircling gears as purse seines whose catchability coefficient is affected by a wide variety of factors (Powles 1981). To demonstrate that the relationship is not gear-specific, we examined the stock-specific catchability coefficients of herring gill nets, a passive gear for which there is a series of catch-rates based on a common effort standard (catch per net-landing). The relevant data are summarized in Table 2. Consistency with expression (5) is also demonstrated by the gillnet data (Fig. 3), and the inverse relationship between q and stock area is best expressed by a power curve whose exponent coefficient is almost identical to that derived for the purse-seine catch-rate data. We now proceed to examine the existence of this inverse relationship and its interaction with stock abundance within a particular stock.

An Instructive Example

We have chosen the population of spring-spawning herring in Fortune Bay (Fig. 1) as a basis for demonstrating the interdependence between q, stock area, and stock abundance. This choice is based not only on the extensive data base relating to the biological characteristics of this stock (Parsons and Hodder 1973; Parsons 1973; Moores and Winters 1979) but also on the fact that the population dynamics of this stock have been described during a period of substantial population change due,

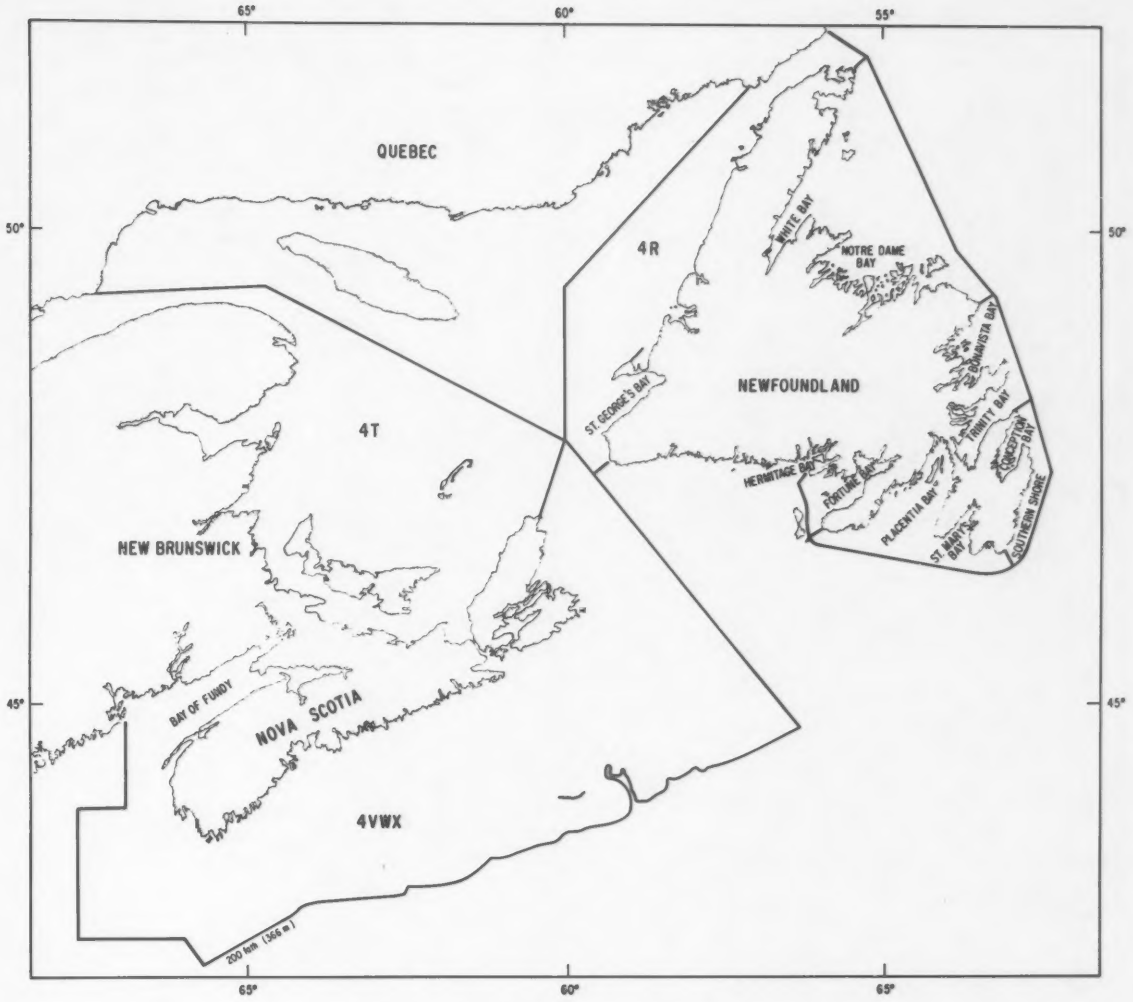

FIG. 1. Location of stock areas mentioned in the text.

TABLE 1. Comparison of abundance and catch-rate (purse seines) characteristics of various herring populations in the Canadian Atlantic area. Exploitable biomass is defined as the sum of the fully recruited biomass plus that portion of the age-specific biomass of recruiting age groups defined by the ratio of their fishing mortality rates to the fully recruited fishing mortality rate.

Stock	Period	Area of stock (km^2)	Mean exploitable biomass (kt)	Mean catch rate (t/d)	Catchability coefficient (q)	Data source
White Bay –						Winters and Moores 1977
Notre Dame Bay	1975–76	21 900	110	91	0.00083	Wheeler and Winters 1981
Bonavista Bay	1975–76	3 950	60	114	0.00190	Winters and Moores 1977
Trinity Bay	1975–76	3 750	25	87	0.00348	Winters and Moores 1977
Fortune Bay	1967–74	3 600	20	54	0.00270	Winters et al. 1985
Western Newfoundland	1970–76	30 900	210	57	0.00027	Tremblay et al. 1983
Southern Gulf	1971–76	79 250	180	42	0.00023	Winters and Moores 1980
Bay of Fundy	1970–76	122 000	400	46[a]	0.00012	Sinclair et al. 1982

[a]Catch per night.

TABLE 2. Comparison of abundance and catch-rate (gill nets) characteristics of various herring populations in the Canadian Atlantic area.

Stock	Period	Area of stock (km^2)	Mean exploitable biomass (kt)	Mean catch rate (kg/d)	Catchability coefficient (q)	Data source
White Bay – Notre Dame Bay	1979–80	21 900	32.5	48.0[a]	0.00148	Wheeler and Winters 1981
Bonavista Bay	1979–80	3 950	19.5	83.0[a]	0.00426	Wheeler and Winters 1981
Trinity Bay	1979–80	3 750	7.5	85.9[a]	0.01145	Wheeler and Winters 1981
Conception Bay	1979–80	5 400	2.5	31.3[a]	0.01252	Wheeler and Winters 1981
St. Mary's Bay – Placentia Bay	1979–80	9 820	10.0	34.6[a]	0.00346	Moores et al. 1981
Fortune Bay	1979–80	3 600	2.8	20.9[a]	0.00745	Winters et al. 1985
Western Newfoundland	1979–80	30 900	90.0	92.0[a]	0.00102	Trembley et al. 1983
Southern Gulf	1973–80	79 250	105.0	82.4[b]	0.00078	Cleary 1982

[a]Spring fishery.
[b]Spring and fall fishery.

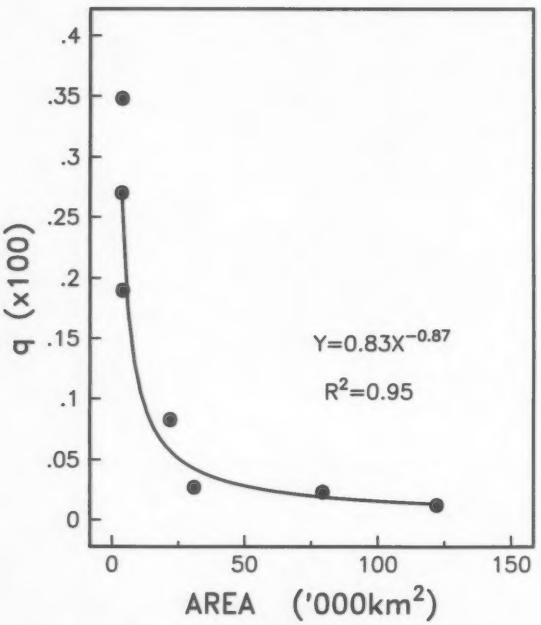

FIG. 2. Catchability coefficient (q) of the large purse-seine fleet and stock area for various Northwest Atlantic herring stocks (see Table 1 for source details).

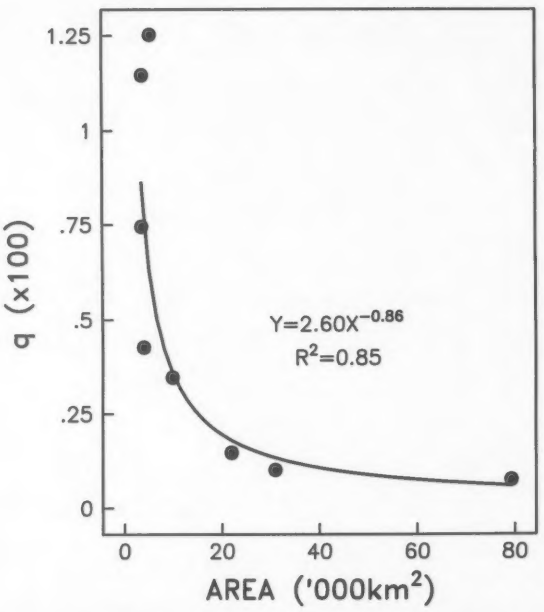

FIG. 3. Catchability coefficient (q) of herring gill nets and stock area for various Northwest Atlantic herring stocks (see Table 2 for source details).

in large part, to the fishing activities of a purse-seine fleet that exploited this stock during a consistent period of the year (Winters et al. 1985).

Annual Fishing Patterns 1967–74

The large Atlantic purse-seine fleet began a winter (January–April) fishery in Fortune Bay in 1967 (Winters et al. 1985) and maintained significant catches in that area until 1974. Logbook records and interview reports are available for this period and contain sufficient detail to identify the location of most reported fishing sets whereas information on the area searched and time searched is much more limited and usually in insufficient detail.

We subdivided Fortune Bay into a grid of 3.3 × 3.3 km squares and, from logbook records, plotted for each year the distribution and intensity of purse-seine fishing effort in terms of fishing sets. The results (Fig. 4 and 5) indicate that when the fishery began in 1967, effort was concentrated mainly at the head of Fortune Bay in the Bay L'Argent – Terrenceville area. Considerable expansion of the purse-seine fishery occurred in 1968 although fishing effort was again mostly concentrated at the head of the bay. The range of the fishery decreased in 1969, particularly at the western extremes, and a shift in fishing effort to Long Harbour and Belleoram occurred. This westward shift in fishing effort continued in 1970 although the range of the area fished remained extensive. By 1971 there was a substantial

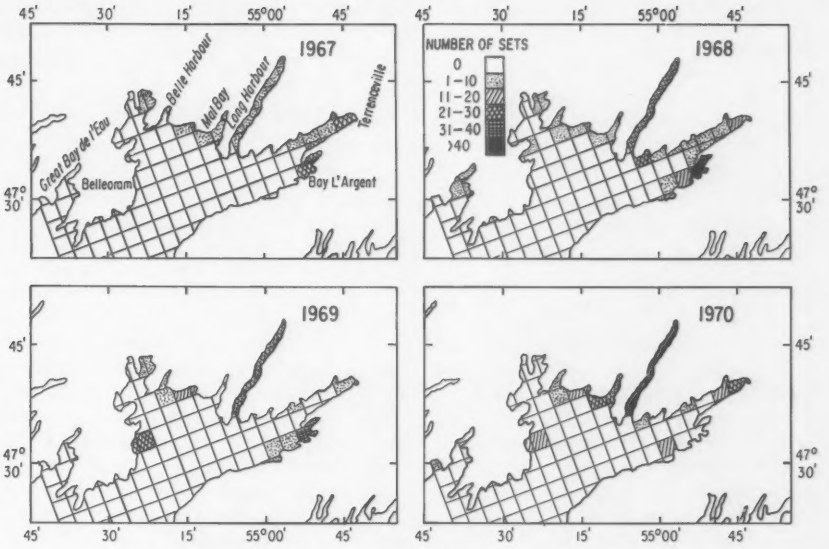

FIG. 4. Distribution of fishing effort (in terms of fishing sets) of the large purse-seine fleet in Fortune Bay, 1967–70.

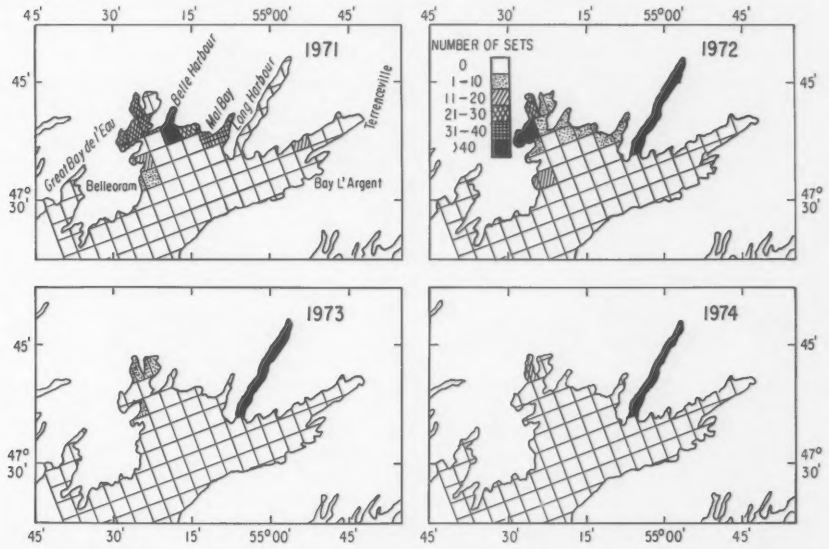

FIG. 5. Distribution of fishing effort (in terms of fishing sets) of the large purse-seine fleet in Fortune Bay, 1971–74.

reduction in both the eastward and westward limits of the applied fishing effort, and a further attrition in the eastward limits of fishing effort occurred in 1972 when most of the fishing effort was concentrated in the Long Harbour and Cinq Island Bay area. In 1973 an additional reduction in the westward limit of the fishery was evident, and this continued into 1974 when nearly all of the fishing effort was concentrated in the Long Harbour area. In summary, these data indicate that there was a substantial reduction in the area fished by the purse-seine fleet in Fortune Bay during the 1970's.

Catch-Rate Characteristics

Catch-rate data of the purse-seine fleet are available from interview reports and log records for the period 1967–74. These data have been analyzed by Winters et al. (1985) for the period 1967–73 in terms of fishing effort defined as the standard operating day (i.e. time between departure from and return to landing port, excluding down time). Such analyses have been extended in this paper to include additional data from 1974 and an alternative, more precise expression of fishing effort in

TABLE 3. Regression coefficients of purse-seine monthly catch-rates as calculated by the multiplicative model of Gavaris (1980).

Month	Catch per set[a]	Catch per standard operating day[b]
January	0.000	0.000
February	−0.165	−0.067
March	−0.258	−0.141
April	−0.479	−0.462

[a]F value = 37.8 (3 df); $p < 0.05$.
[b]F value = 66.3 (3 df); $p < 0.1$.

terms of fishing sets. For both expressions of fishing effort the multiplicative model of Gavaris (1980) indicates significant seasonality factors (Table 3) which have been taken into account through the Gavaris (1980) standardization procedure. These standardized catch-rates (Tables 4 and 5) indicate similar trends in abundance and suggest a cycling downwards of abundance since 1967. A similar trajectory of population change is indicated by cohort analysis (Winters et al. 1985) with the exception that population decline continues after 1973 rather than increases, as indicated by catch-rate data. Searching success, measured as the ratio of searching time (operating days (Table 5)) to fishing time (number of sets (Table 4)), was not correlated with stock abundance (Fig. 6) as estimated by cohort analysis. This may reflect a systematic bias in the catchability coefficient of the purse-seine fleet in Fortune Bay and/or that the measure of searching time (operating days) was so crude that it overshadowed any real changes in that parameter. To avoid this ambiguity in fishing effort we confine our estimates of fishing effort to the number of fishing sets which are more precisely known.

Interrelationship Between Catch-Rates and Population Change

Although logbook records contained insufficient detail on the area searched, general comments by the fishing captains indicated that in all years the area searched extended well beyond the areas in which herring concentrations were found and fished. In addition, Fortune Bay is such a small area that a single vessel could easily search the entire bay in a single day. We have therefore assumed that the spatial distribution of fishing effort shown in Fig. 4 and 5 is representative of the changes in the area occupied by herring in Fortune Bay during their overwintering phase in the period 1967–74. We have defined the area within the limits of this spatial distribution as the "stock range" and these data are summarized in Table 6 along with estimates of stock biomass (from Winters et al. 1985) and values for annual catchability coefficients defined as the ratio of catch-rate (tons per set) to exploitable biomass. From such data we can now examine the interdependence between catch-rate, stock abundance, and stock area.

There is a positive nonlinear relationship between the stock range and stock abundance of Fortune Bay herring (Fig. 7). This nonlinearity is consistent with our expectations and with the observations of Blaxter and Holliday (1963). The 1967 value for stock range appears anomalous and was excluded from further analysis. This exclusion is considered justifiable on the basis that 1967 was the first year of the purse-seine fishery in Fortune Bay and therefore it is likely that a learning factor was involved

TABLE 4. Catch-rate data of the purse-seine fleet operating in Fortune Bay during the period 1967–74. Numbers in parentheses refer to the effort (number of sets).

Year	Catch per set (t)				Standard catch rate (Jan.–Apr.)	Estimated total effort (sets)
	Jan.	Feb.	Mar.	Apr.		
1967	—	—	—	45.0 (56)	70.5	80
1968	54.6 (1)	53.0 (72)	51.2 (65)	50.1 (35)	69.5	212
1969	58.2 (26)	16.4 (5)	—	—	50.2	138
1970	94.2 (8)	32.8 (12)	30.6 (19)	0.0 (1)	47.5	198
1971	50.3 (19)	67.0 (30)	29.6 (4)	27.3 (3)	64.7	232
1972	55.6 (14)	18.2 (2)	44.7 (25)	13.8 (9)	47.5	222
1973	14.9 (15)	69.0 (16)	41.0 (1)	54.6 (1)	26.6	122
1974	—	—	—	34.4 (22)	51.3	44

TABLE 5. Catch-rate data of the purse-seine fleet operating in Fortune Bay during the period 1967–74. Numbers in parentheses refer to the effort (in operating days).

Year	Catch per day (t)				Standard catch rate (Jan.–Apr.)	Estimated total effort (days)
	Jan.	Feb.	Mar.	Apr.		
1967	—	—	—	41.5 (35)	64.4	88
1968	—	64.6 (67)	55.2 (70)	33.8 (51)	63.4	232
1969	62.3 (45)	34.8 (31)	47.6 (3)	—	51.1	134
1970	67.0 (57)	49.7 (25)	60.4 (40)	79.6 (67)	67.7	139
1971	48.3 (103)	59.4 (58)	50.4 (96)	32.6 (31)	55.8	269
1972	44.9 (75)	49.0 (11)	31.7 (128)	22.5 (68)	39.7	266
1973	22.1 (24)	22.1 (21)	18.7 (2)	38.3 (3)	25.3	129
1974	—	—	—	38.5 (43)	60.2	38

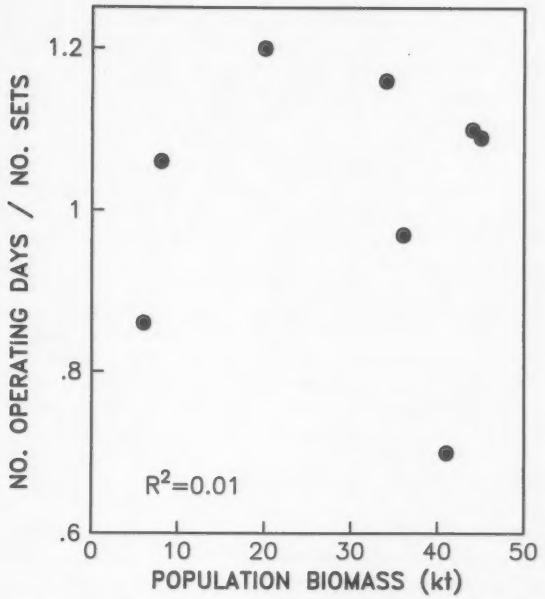

FIG. 6. Searching success (i.e. searching time per set) and population abundance of Fortune Bay herring, 1967–74.

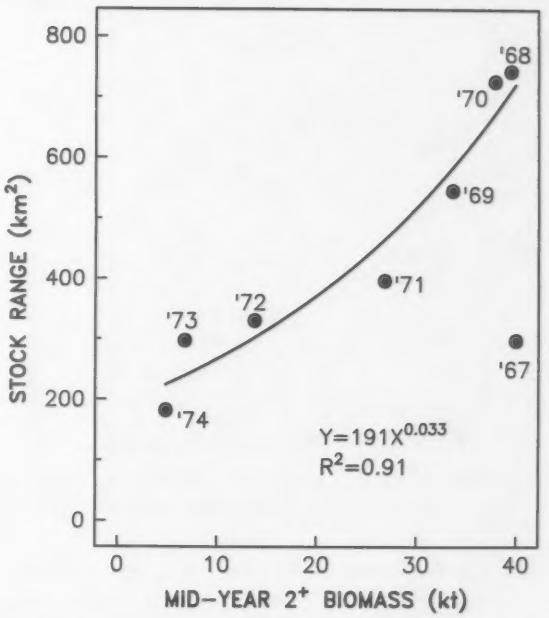

FIG. 7. Stock range and population biomass of Fortune Bay herring.

TABLE 6. Biomass, catchability coefficient (q), and stock range of Fortune Bay herring, 1967–74.

Year	Mid-year 2+ biomass (kt)	q	Stock range (km^2)
1967	39.9	0.00246	297
1968	39.4	0.00275	743
1969	33.5	0.00207	545
1970	37.8	0.00192	726
1971	26.7	0.00392	396
1972	13.7	0.00593	330
1973	6.7	0.00578	297
1974	4.8	0.01655	182

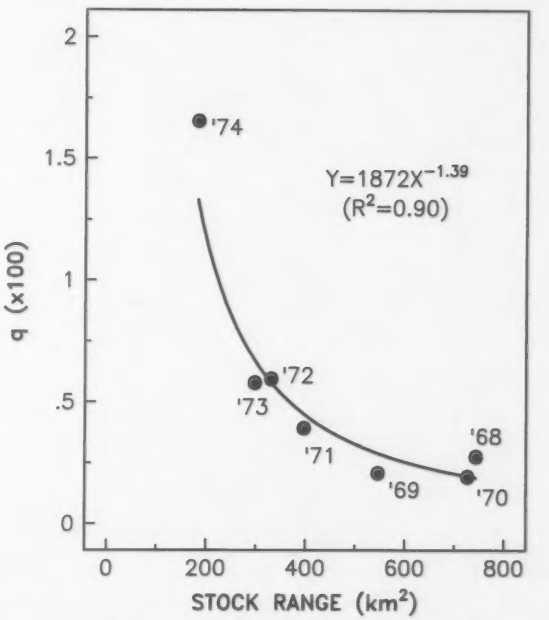

FIG. 8. Catchability coefficient (q) and stock range of Fortune Bay herring (the 1967 data point is excluded).

in similar fashion as was documented for the same fleet fishing along southwest Newfoundland (Winters and Hodder 1975) in 1967. Analysis of temporal variations in the catchability coefficient of the purse-seine fleet indicates that q is negatively correlated with "stock range" (Fig. 8), which is in accordance with the theoretical expectations as described in expression (4). Furthermore, the exponent of the relationship is significantly different than unity ($p < 0.01$) and supports the evidence from Fig. 7 and our hypothesis that the relationship between q and A will be as described in expression (5). This nonlinearity in the relationship of the catchability coefficient to stock area is an important property of q, since it implies that larger changes in q will occur at the lower stock levels when the need for unbiassed stock indices is most critical. The bias that this relationship imparts to commercial catch-rate data will likely cause such indices to substantially underestimate both the rate of decline and the rate of recovery of a depleted fish stock.

We conclude that the catchability coefficient of the purse-seine fleet in Fortune Bay during the period 1968–74 was a direct function of the area occupied by the herring stock, which was itself a density-dependent function of population abundance. This implies, of course, that q is an indirect density-dependent function of stock abundance and will probably be of the form $q = kN^{-g}$ (Ulltang 1976); unfortunately we cannot test this proposition due to the absence of an independent stock abundance index of Fortune Bay herring.

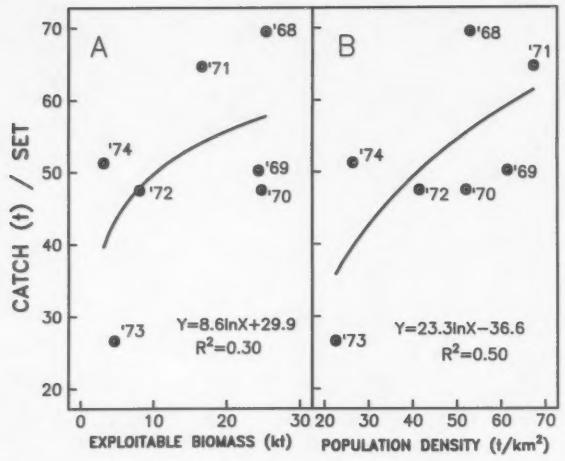

FIG. 9. (A) Catch-rate (catch per set) and exploitable biomass and (B) catch rate (catch per set) and population density of Fortune Bay herring.

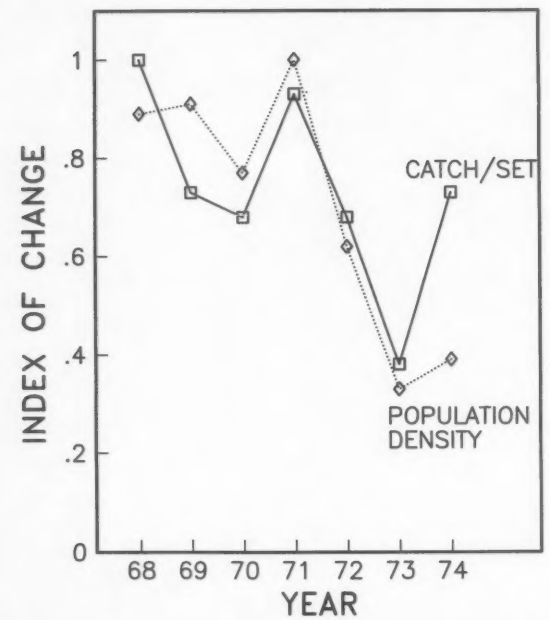

FIG. 10. Time-series trends in school size (catch per set), population density (biomass/km), and population biomass of Fortune Bay herring.

Catch-Rates, Population Abundance, and School Size

The inverse relationship between the catchability coefficient and stock area (Fig. 8) of Fortune Bay herring implies that the purse-seine catch-rate index will be significantly correlated with population density (biomass per area) but not with population biomass. Regression analyses confirm this observation (Fig. 9) although the relationship between catch-rate and population density is barely significant ($p = 0.05$) and best expressed as a logarithmic curve. This weak relationship probably reflects an additional property of the purse-seine catch-rate index relating to school size. Interviews with purse-seine skippers, supported by observations of senior technicians on selected cruises of the large purse-seine fleet during the 1960's and 1970's, suggest that in most cases successful sets capture the entire target of the set. Therefore, catch per set may be used as an index of school size (Ulltang 1980), and we have replotted this catch-rate index in a temporal series along with density (biomass per square kilometre) in Fig. 10. The close correspondence between the track of school size and population density for the years 1968–73 demonstrates that Fortune Bay herring compensated for changes in biomass through a combination of changes in stock area and school size. However, school size increased at a much greater rate between 1973 and 1974 than was evident in the population density. This may reflect the possibility that at very low stock sizes the reduced distributional area occupied by the stock resulted in an overlap of the area searched by individual vessels and/or an overlap of school radii such that school amalgamation occurs (Paloheimo and Dickie 1964). In either case there is a further confounding of the catch-rate index.

Discussion and Conclusions

We have shown that the theoretical expectation of catchability coefficient (q) being inversely proportional to stock area has an empirical basis which is borne out not only through comparisons of q between Atlantic herring stocks but also in the example of Fortune Bay. Fortune Bay herring reacted to depletions in abundance by reducing their distributional range rather than by counterbalancing such abundance changes through commensurate adjustments in density in a constant stock area as is commonly assumed in interpretation of commercial catch-rate data. Furthermore, school size (i.e. catch per set) of Fortune Bay herring also decreased as population biomass declined, which in conjunction with the independence between catch-rates and fishable biomass implies that school numbers probably remained constant. At very low stock levels, however, there may have been a reversal of this response such that school aggregation occurred.

The analyses of Fortune Bay data support our hypothesis that density-dependent changes in stock area will occur in nonlinear fashion and therefore the relationship between q and stock area will be of the form $q = cA^{-b}$. This finding is consistent with observations by Ulltang (1976) and MacCall (1976) that the interaction between q and population abundance of pelagic fish species can be adequately described by the relationship $q = kN^{-g}$. For values of $g > 0$, catch-rates may vary with population abundance but the change will not be proportional; as g approaches 1, catch-rates will become constant and a constant effort will then generate a steadily higher fishing mortality as stock size increases.

The changes in the stock range of Fortune Bay herring in response to population abundance are not unique. The southern Gulf of St. Lawrence herring stock supported a large winter fishery along southwestern Newfoundland and extensive spring, summer, and fall fisheries in the southern Gulf during the 1960's and early 1970's when population levels were high (Winters and Hodder 1975). Since then, biomass levels have decreased substantially and this has been accompanied by the collapse of the southwest Newfoundland winter fishery (Winters and Beckett 1978) and the spring and fall fisheries at the Cabot Strait entrance to the southern Gulf (L. Cleary, pers. comm.). Wheeler and Winters (1984) have shown that tagged herring along eastern Newfoundland exhibited much less dispersion in the early 1980's when population levels were lower than in the

1970's when population levels were higher. Similarly, Dragesund et al. (1980) have shown that the area occupied by the Atlanto-Scandian herring stock shrunk in proportion to changes in stock size. North Sea herring also decreased its distributional area after the mid-1960's when population abundance began to decline (Saville and Bailey 1980). This general response of herring stocks to changes in abundance will result in q being inversely related to stock abundance, and there is ample evidence in the published literature (Pope 1980; Ulltang 1980; Jakobsson 1980; Anthony and Waring 1980) to support this property of q. Furthermore, a variety of other pelagic fish stocks have shown similar interactive changes in area and catchability during periods of rapid population declines. These include the Atlantic menhaden (*Brevoortia tyrannus*) (Shaaf 1980), Pacific sardine (*Sardinops sagax caerula*) (MacCall 1976; Radovich 1979), northern anchovy (*Engraulis mordax*) (Radovich 1976), and Peruvian anchovy (*Engraulis ringens*) (Csirke 1980). These examples, taken together with our analysis of Fortune Bay herring, lead us to conclude that commercial catch-rate data of pelagic fish stocks will usually provide a biassed index of population abundance and this will be particularly so for such active encircling gears as purse seines which superimpose their own varying biasses (Clark and Mangel 1979; Powles 1981) on those dictated independently by stock dynamics. Among dermersel fish stocks, published literature on their distributional responses to changes in abundance is scanty. However, Lear (1984) has noted that the dispersion of tagged cod of the 2J3KL stock was much greater during the 1950's and 1960's (see Templeman 1974) when biomass levels were relatively higher than in the late 1970's when abundance levels of cod were much lower. Gavaris et al. (1984) have shown that the catchability coefficients of 2J3KL cod increased substantially during the 1970's as stock sizes declined. Pope and Garrod (1975) showed that for both Arctic-Norwegian and West Greenland cod there was also an increase in q as stock size became smaller, and ascribed their findings to real changes in stock availability. These observations lead us to conclude that the inverse relationship between q and stock abundance may be a general feature of marine fish populations and that this relationship is probably mediated through systematic changes in stock area. This conclusion strongly supports the findings of Paloheimo and Dickie (1964) who demonstrated, from a theoretical viewpoint, that fishing success depended not only on the abundance of fish but more importantly on their distribution. Thus, commercial catch-rates, even when measured with the utmost precision, are likely to be biassed and should be used with caution particularly as a means of calibrating sequential population models; instead, emphasis should be placed on research vessel survey data collected in a standard manner and covering the distributional area of the stock.

The mechanism responsible for fish populations expanding or contracting their distributional range as abundance varies is poorly understood, although a variety of models have been developed that assume that such a response is related to a behavioural tendency towards maintaining an optimum density per unit area (Pope and Garrod 1975). It has been argued, for example, that such behaviour has evolved in response to specific selection pressures such as predator avoidance (Radovich 1979). There is, however, another feature of stock range variations that may be related to the demographic compositions of the population. Large, unexploited populations have a predominance of older, larger fish, and since swimming speed is a power function of fish length (Yates 1983), these fish will tend to migrate farther than smaller fish which are usually characteristic of depleted populations. This type of distributional response was exhibited by southern Gulf of St. Lawrence herring whose overwintering migration rates were a direct positive function of age (Winters and Hodder 1975). Similar findings have been reported for Atlanto-Scandian herring (Dragesund et al. 1980), southern Gulf of St. Lawrence cod (Jean 1964), and Arctic-Norwegian cod (Trout 1957). In the example of Fortune Bay herring there was an order of magnitude decrease in the number of large (age 7 and older) herring from 1968 to 1974. We suggest that this reduction in the numbers of larger herring was responsible, at least in part, for the observed reductions in the range of Fortune Bay herring during the period 1968–74.

Finally, we reemphasize the significance of the inverse relationship between catchability and stock area; i.e. a unit of fishing effort will generate a higher fishing mortality and a higher catch-per-unit-effort in a small area compared with these same parameters in a larger area. The general occurrence of this observation is not only evident in marine fish populations (as we have demonstrated) but it also applies to freshwater populations where it has been generally shown that small lakes are more efficiently exploited per unit surface area than large lakes when both are subjected to proportionally similar fishing effort (Ryder et al. 1974).

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Responses of Sea-Ice Microalgae to Climatic and Fortnightly Tidal Energy Inputs (Manitounuk Sound, Hudson Bay)[1]

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Variations of sea-ice microalgae at the ice–water interface (Manitounuk Sound, Hudson Bay, Canada) were studied in relation to various energy inputs (light, tidal mixing, and heat) in April and May 1982. Seasonal photosynthetic activity does not start before the light intensity reaches 7.6 $\mu Einst \cdot m^{-2} \cdot s^{-1}$. Above this value, the seasonal increase in cell numbers and chlorophyll and in the photoadaptation index (I_k) is related to the increase in underice light intensity.The sea-ice community changes from shade to light adaptation to optimize the use of ambient light energy. Photosynthetic efficiency (α^B) is mainly controlled by the fortnightly tidal vertical mixing, which governs the amount of phosphate (or of another nutrient factor) in the upper brackish layer. The ice microflora, which grows at a stable interface, takes advantage of nutrient replenishment during mixed water column conditions. We conclude that production of microalgae depends upon three forms of energy: (1) the flux of solar light, (2) the inputs of auxiliary mechanical energy (here, the fortnightly tides), and (3) the energy exchanges (here, the heat flux) responsible for the maintenance or destruction of energetic interfaces (ergoclines).

Les variations de la microflore des glaces (détroit de Manitounuk, baie d'Hudson, Canada) à l'interface glace–eau, ont été étudiées en relation avec différents apports d'énergie (lumière, mélange par la marée et chaleur), en avril et mai 1982. L'activité photosynthétique saisonnière de la microflore ne débute que lorsque l'intensité lumineuse atteint 7,6 $\mu Einst \cdot m^{-2} \cdot s^{-1}$. Au delà de ce seuil, l'augmentation saisonnière du nombre de cellules, de la chlorophylle ainsi que du paramètre de photoadaptation (I_k) est liée à l'augmentation d'intensité lumineuse sous la glace. La communauté des glaces passe d'un caractère sciaphile à un caractère héliophile, de façon à optimiser l'utilisation de l'énergie lumineuse ambiante. L'efficacité photosynthétique (α^B) est principalement contrôlée par le mélange vertical (marées semi-mensuelles), qui détermine la teneur des eaux saumâtres superficielles en phosphate ou autre facteur nutritif. La microflore des glaces, qui croît à une interface stable, est avantagée par l'approvisionnement en éléments nutritifs, durant les périodes de mélange. On en conclut que la production des microalgues, dépend de trois formes d'énergie : (1) le flux d'énergie solaire, (2) les apports d'énergie mécanique auxiliaire (ici, la marée semi-mensuelle) et (3) les échanges d'énergie (ici, la chaleur) responsables du maintien ou de la destruction des interfaces énergétiques (ergoclines).

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Sea ice can support large concentrations of unicellular microalgae (epontic community), as reported for the Antarctic by Bunt (1963), Bunt and Wood (1963), Bunt and Lee (1970), Palmisano and Sullivan (1983), and McConville and Wetherbee (1983) and for the Arctic by Apollonio (1961, 1965), Meguro et al. (1966, 1967), and Horner and Schrader (1982). Hypotheses used to explain the presence of these microalgal communities in sea ice are (1) the trapping of microalgal cells in the seawater as it freezes (Meguro et al. 1967; Horner 1976), or (2) the trapping of cells by the ice crystals (frazil) in the water column that float to the surface and are incorporated into the ice cover (Garrison et al. 1983). Both hypotheses associate the epontic community with the growth of ice, a factor that could explain the observed vertical distribution of epontic cells in sea ice (Poulin et al. 1983; Demers et al. 1984). Chlorophyll *a* concentrations are much higher in the ice than in the underlying water column (Clarke and Ackley 1984; Demers et al. 1984). During spring, there is growth and division of the epontic cells in addition to the mechanical accumulation of microalgae (Horner 1976). These biological processes are significantly influenced by the physical structure of the ice (Clarke and Ackley 1984).

Light is a critical factor in growth regulation of ice microflora

[1]Contribution to the program of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec).

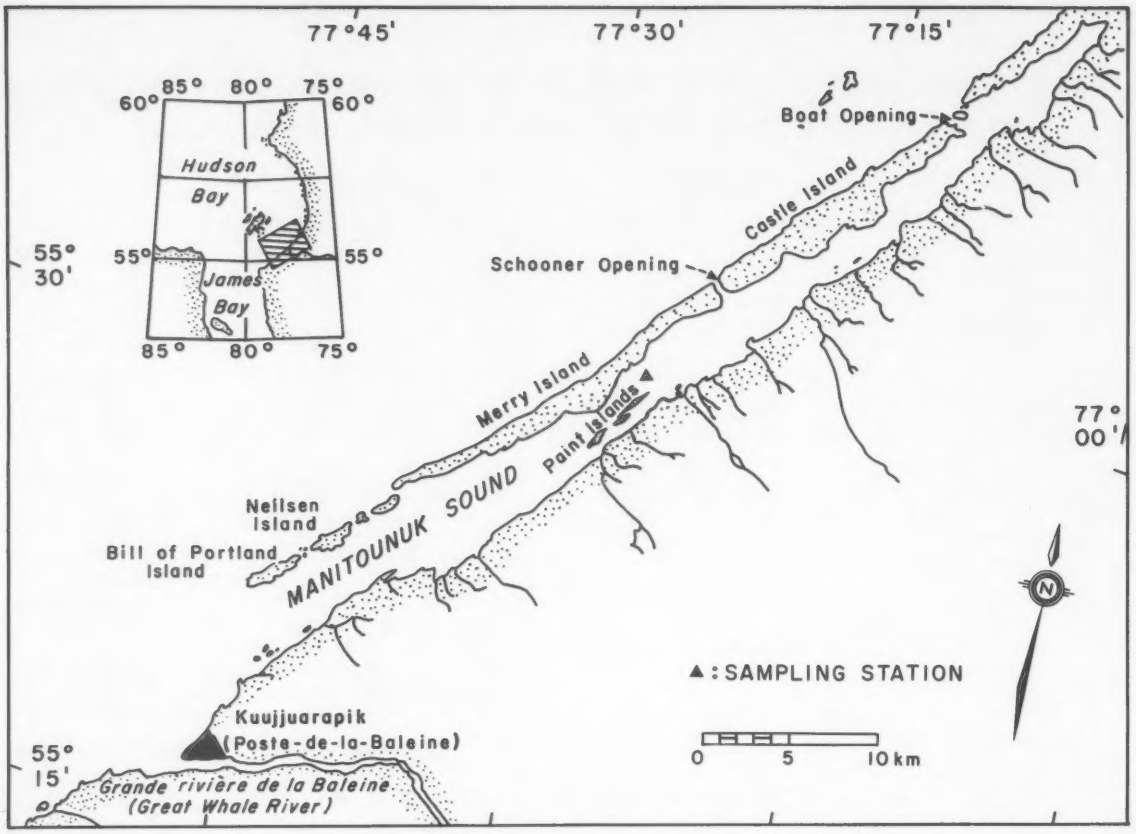

FIG. 1. Sampling area showing the location of the sampling station.

(Meguro et al. 1967; Bunt and Lee 1970; Clasby et al. 1976; Grainger 1979; Hsiao 1980; Horner and Schrader 1982), which are adapted to the low light intensities prevailing under the ice (Bunt 1964). Nutrients are replenished by exchanges between the lower part of the ice and the underlying water, by desaltation, or by in situ bacterial activity (Meguro et al. 1967; Alexander et al. 1974; Sullivan and Palmisano 1981). Numerous observers have stated that nutrients probably do not limit the epontic community (Meguro et al. 1967; Bunt and Lee 1970; Alexander et al. 1974; Grainger 1977; Sullivan and Palmisano 1981; Horner and Schrader 1982; Poulin et al. 1983; Clarke and Ackley 1984).

In this study, we examine how microalgal growth is controlled by the various forms of energy (light, tidal mixing, heat) that shape the ice–water interface. To do so, we first identify the climatic and hydrodynamic factors that control microalgal growth at that interface in spring. Then, we define the mechanisms that relate growth to energy through the agency of the ice–water environmental factors.

Materials and Methods

Physical characteristics of Manitounuk Sound (southeastern Hudson Bay) and of the sampling station (Fig. 1) are given by Ingram (1983) and Poulin et al. (1983). Our sampling station corresponds to their station 1.

From 22 March to 14 May 1982, water temperature, salinity, current velocity, and direction were recorded every 10 min using Aanderaa current meters moored at depths of 1.5 and 8 m from the ice surface. The data record at 8 m was incomplete from 22 March to 16 April. These data were used to calculate the Richardson number ($R\hat{i}$) (Turner 1973), which compares the stabilizing influence of density stratification to the destabilizing effect of velocity shear, and is therefore an approximate index of vertical stability of the water column over the depth interval sampled. Richardson numbers were computed from hourly smoothed data, and then low-pass filtered by moving average (half-amplitude frequency: $0.015 \cdot h^{-1}$) to remove semidiurnal and diurnal variations (Godin 1972).

From 26 March to 16 May 1982, the station was occupied every 3–4 d. Snow depth, ice thickness, air temperature, and light intensity above (I_0) and under (I_z) the ice (Biospherical Scalar Irradiance Meter) were recorded. Water samples were collected from the ice (SIPRE ice corer: 7.5 cm int. diam.) and in the underlying water column (1.7-L Niskin bottles at 0.5, 2, and 10 m). The bottom 20 cm of the ice core was collected, as well as 3 L of the unconsolidated ice mixed with water, sampled in the coring hole at the ice–water interface. Water as well as melted ice samples were filtered on Whatman GF/C for the fluorometric determination of chlorophyll *a* and pheopigments (Yentsch and Menzel 1963) after a 1-h extraction in 100% methanol at 0°C (Holm-Hansen and Riemann 1978). The filtrate

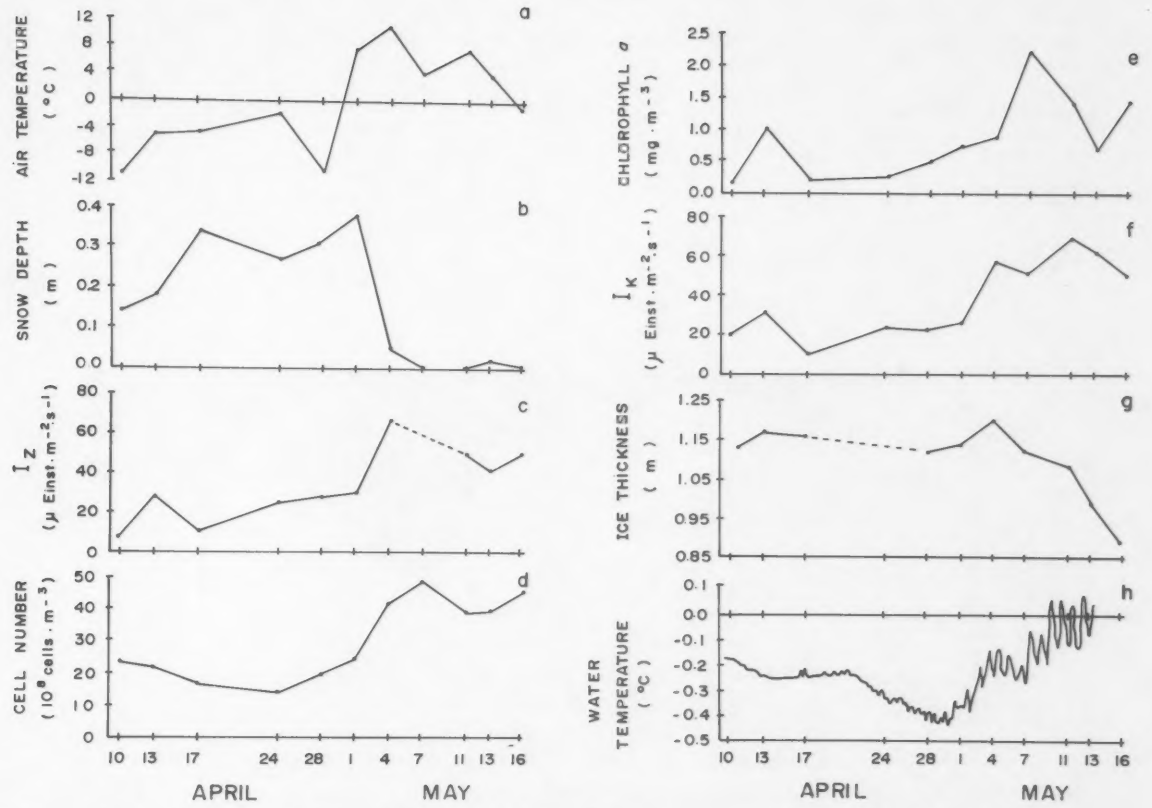

FIG. 2. Seasonal variation of (a) air temperature, (b) snow depth, (c) underice light intensity (I_z), (d) cell number, (e) chlorophyll *a* concentration, (f) photosynthetic photoadaptation index (I_k) at the ice–water interface, (g) ice thickness, and (h) water temperature 1.5 m below the ice surface.

was frozen for later determination of nutrients (NO_2 + NO_3, NH_4, PO_4, SiO_3) using a Technicon autoanalyzer (Strickland and Parsons 1972). Samples were preserved with acidic Lugol for species enumeration (Utermöhl 1931). Diatom species diversity was computed using Shannon's entropy *H* (Legendre and Legendre 1983). Salinities were measured with a Hytech 6220 salinometer. Parameters of the photosynthesis versus irradiance curves were computed (Jassby and Platt 1976) from 125-mL samples of the ice–water interface, incubated with 0.185 MBq $H^{14}CO_3^-$ under 10 light intensities (3.2, 8.6, 19.3, 26.8, 42.9, 53.6, 58.9, 71.8, 78.2, and 107.2 μEinst·m^{-2}·s^{-1}) in Hawaiian incubators (Doty and Oguri 1959). The dark bottle was replaced by a bottle with added DCMU (Legendre et al. 1983). After 2-h incubations, 50 mL from each incubated sample was filtered through Nuclepore 0.4-μm filters, which were then frozen for later determination of activity by liquid scintillation (Pugh 1973) after addition of 0.5 mol HCl·L^{-1} to the scintillation vials (Lean and Burnison 1979). Computed photosynthetic parameters, normalized per unit chlorophyll *a*, are the photosynthetic capacity (P^B_{max}), the photosynthetic efficiency (α^B), and the photoadaptation index ($I_k = P^B_{max}/\alpha^B$).

As no significant photosynthetic activity was observed prior to 10 April, only those data from 10 April to 16 May 1982 are plotted in the figures and tables. Nonparametric rank statistics were used to analyze the data: Kendall's rank correlation coefficient (τ), partial τ, and Friedman's two-way analysis of variance to compare nutrient concentrations at the various sampling dates and depths (Siegel 1956). The least-squares fit of a second-order polynomial was used to remove the trend in the PO_4 and α^B series.

Results

In Manitounuk Sound, most of the physical environmental characteristics of the ice–water interface show definite seasonal patterns (Fig. 2a–2c), their variations being thus well correlated with the time of the year (Table 1). The seasonal increases in cell numbers (Fig. 2d) and chlorophyll *a* (Fig. 2e) are mainly related (Table 1) to the seasonal increase in underice illumination (I_z, Fig. 2c), which is itself correlated (Table 1) with air temperature and snow depth (Fig. 2a, 2b). No significant carbon assimilation by microalgae was measured before I_z reached the critical value I_{crit} = 7.6 μEinst·m^{-2}·s^{-1} on 10 April. A significant increase in biomass was recorded only when I_z reached ~20 μEinst·m^{-2}·s^{-1} (Fig. 2a–2e). Above I_{crit}, the photoadaptation index (I_k, Fig. 2f) followed changes in underice illumination (I_z, Fig. 2c), I_k and I_z being highly correlated (Table 1). In addition, $I_k \approx I_z$ since $I_z/I_k \approx 0.95$.

Small naked flagellates dominate cell numbers at the ice–water interface, as they make up between 46 and 98% of the counts (Fig. 3a). Pennate diatoms dominate the larger forms, with an average 17% of the total cells. Typical planktonic taxa (centric diatoms and pyrrophytes) do not exceed, on the average, 3% of the cells. Among pennate diatoms, *Nitzschia frigida*,

TABLE 1. Kendall's rank correlation coefficients between physical and biological variables measured at the ice–water interface from 10 April to 16 May 1982 (numbers of observations $N = 11$; pairwise deletion of missing data; $*0.01 < p \leq 0.05$, $**p \leq 0.01$).

Air temperature	Snow depth	Ice thickness	I_z	Cell number	Chl *a*	I_k	Diatom diversity	
0.491*	−0.411	−0.584*	0.644**	0.527*	0.564*	0.564*	0.587*	Time of year
	−0.187	0.0	0.600*	0.309	0.418	0.636**	0.514*	Air temperature
		0.396	−0.450	−0.598*	−0.486*	−0.561*	−0.208	Snow depth
			−0.111	−0.315	−0.180	−0.225	−0.056	Ice thickness
				0.644**	0.778**	0.733**	0.450	I_z
					0.600**	0.455	0.440	Cell number
						0.564*	0.367	Chl *a*
							0.477*	I_k

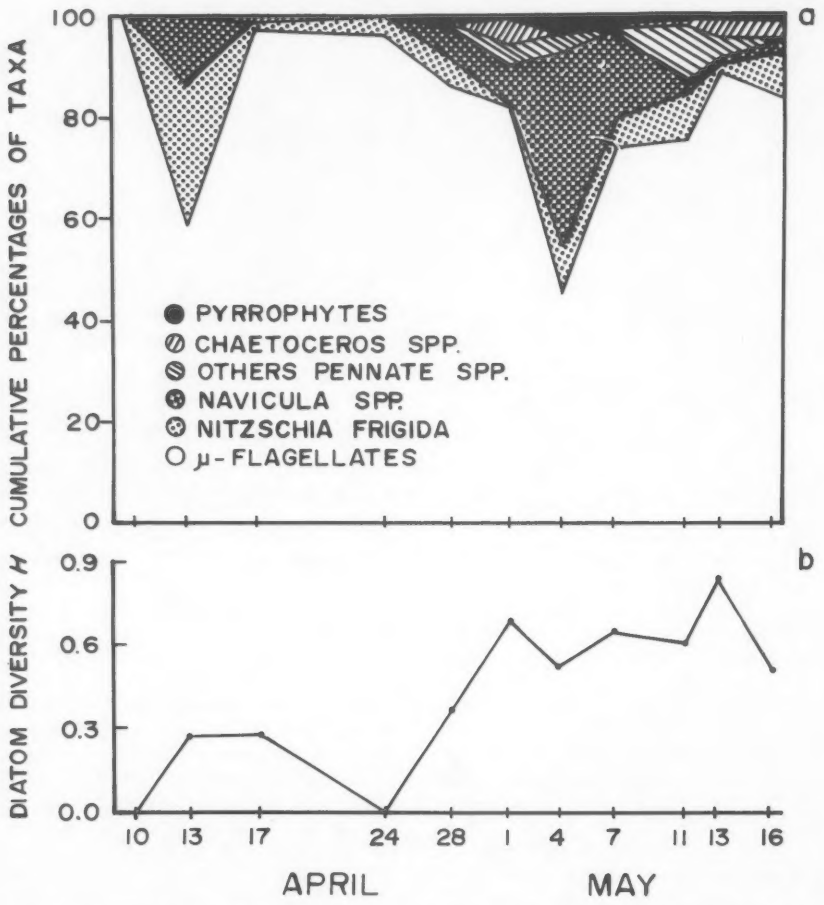

FIG. 3. Seasonal variations of (a) taxonomic composition and (b) diatom species diversity H at the ice–water interface.

which persists throughout the season, and *Navicula* species account respectively for 38 and 58% of the cells; other pennate diatoms belong mainly to the genera *Nitzschia*, *Diploneis*, *Pinnularia*, and *Entomoneis*. All the centric diatoms belong to the genus *Chaetoceros*.

The index of diatom species diversity shows a very definite seasonal pattern (Fig. 3b), and is correlated with the time of the year (Table 1). Diatom diversity is also directly correlated with the photoadaptation index (I_k, Table 1). However, the partial correlation between diversity and I_k, when controlling for the time of the year, is $\tau = 0.244$. This low partial correlation is consistent with a double effect model, where the time of the year would cause variations in both diversity and I_k (Legendre and Legendre 1983). This would indicate that variations in I_k are not caused by changes in species diversity.

On a shorter time scale, the Richardson number ($R\hat{i}$, Fig. 4a)

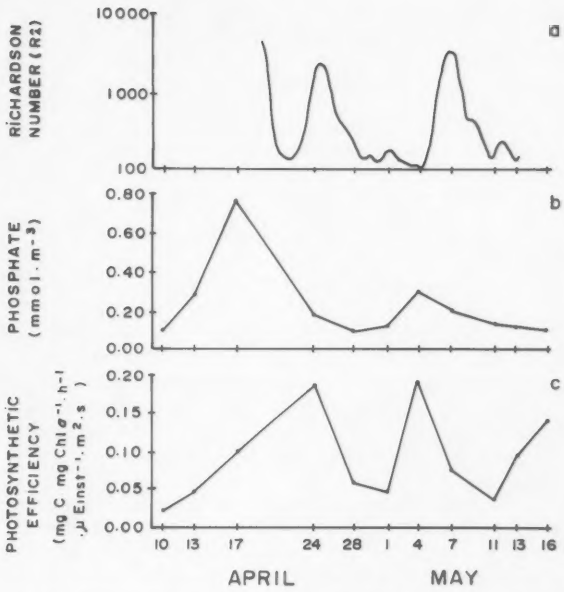

FIG. 4. Fortnightly variations of (a) Richardson number (low-pass), (b) phosphate concentration, and (c) photosynthetic efficiency (α^B) at the ice–water interface.

TABLE 2. Rank correlation coefficients (upper triangle) and partial rank correlation coefficients (lower triangle) between detrended photosynthetic efficiency (α^B), detrended phosphate concentration at the ice–water interface, and Richardson number ($\overline{Ri}$: 13-h average, measured five semidiurnal tidal cycles before α^B and PO_4) (number of observations $N = 7$; $*0.01 < p \leq 0.05$, $**p \leq 0.01$).

	$\overline{Ri}$	PO_4	α^B
$\overline{Ri}$		−0.714*	−0.810*
PO_4	0.076		0.905**
α^B	−0.550	0.796	

exhibits fortnightly variations, as does the photosynthetic efficiency (α^B, Fig. 4c). By averaging the low-pass $\overline{Ri}$ values over 13-h intervals, the new values were found to have a significant inverse relationship with α^B, by including a time lag of five semi-diurnal tidal cycles (Table 2). However, this correlation did not seem to hold when controlling for the effect of PO_4 (Table 2: the significance of partial τ cannot be tested). This might indicate that PO_4 intervenes in the relationship between $\overline{Ri}$ and α^B (Legendre and Legendre 1983).

A Friedman's two-way analysis of variance showed that the four measured nutrients had a highly significant ($p < 0.001$) heterogeneous vertical distribution throughout the sampling period (Table 3). Conover's (1980) a posteriori tests can be used to identify the sampling levels where nutrient concentrations were higher. Ammonia was more abundant in the lower 20 cm of the ice as well as at the ice–water interface and at 0.5 m than lower in the water column; nitrate (plus nitrite) and silicate were less abundant in the lower 20 cm of the ice than at the ice–water interface and in the water column; waters under the pycnocline (>2 m) were richer in phosphate than those above. Phosphate concentrations were positively correlated with salinity ($\tau = 0.45$, $p < 0.001$).

The increase in air temperature at the beginning of May (Fig. 2a) was initially accompanied by a thinning of the ice cover (Fig. 2g) and was followed by a progressive decrease in chlorophyll *a* concentrations at the ice–water interface (Fig. 2e). Throughout this same period, 24-h variations in water temperature due to solar heating were observed at a depth of 1.5 m (Fig. 2h).

Discussion

Seasonal Variations

Maximum concentrations of cells and chlorophyll *a* in Manitounuk Sound were observed on 7 May at the ice–water interface (Fig. 2) and also in the bottom 20 cm of the ice (12×10^8 cells·m^{-2} and 0.85 mg Chl *a*·m^{-2}). At this same station, Poulin et al. (1983) reported maximum values of similar magnitude for May 1978: 3.6×10^8 cells·m^{-2} and 0.76 mg Chl *a*·m^{-2}. These are much lower than published chlorophyll concentrations in other Arctic areas: 12.1 mg·m^{-2} in Robeson Channel, Canada, and 12.5 mg·m^{-2} in Barrow Strait and Austin Channel, Canada (Dunbar and Acreman 1980); 23 mg·m^{-2} in Jones Sound, Canada (Apollonio 1965); 26.5 mg·m^{-2} in Narwhal Island, Alaska (Horner and Schrader 1982); 30.1 (Hsiao 1980) and 19.6 mg·m^{-2} (Grainger and Hsiao 1982) in Frobisher Bay, Canada; 30.5 mg·m^{-2} in Barrow, Alaska (Clasby et al. 1973). According to Poulin et al. (1983), water salinity influences both the ice thickness and the efficiency of cell settlement, these being the factors that control the epontic biomass. The low salinity of the water underlying the ice (mean salinity of 4.94 at 1.5 m depth in April–May 1982) is a possible reason for the low biomass of the epontic community in Manitounuk Sound. Contrary to what had been observed by Legendre et al. (1981) at this same station in mid-May 1978, there was no phytoplankton bloom recorded in our samples, as *Chaetoceros* and pyrrophytes did not show any significant increase (Fig. 3).

Seasonal photosynthesis at the ice–water interface does not start in Manitounuk Sound before at least 7.6 μEinst·m^{-2}·s^{-1} diffused through the ice and snow cover (Fig. 2c, 2e). Similar critical light intensities (I_{crit}) have been reported for other polar environments. In the Arctic, they are 2.3–9.3 μEinst·m^{-2}·s^{-1} in Barrow, Alaska (Alexander et al. 1974; Clasby et al. 1976) and 7.7 μEinst·m^{-2}·s^{-1} in Narwhal Island, Alaska (Horner and Schrader 1982). In the Antarctic, the reported I_{crit} values are lower: approximately 0.5–0.9 μEinst·m^{-2}·s^{-1} in McMurdo Sound (Bunt 1964) and ≤0.3 μEinst·m^{-2}·s^{-1} (Palmisano and Sullivan 1983). This difference between Arctic and Antarctic may be related to differences in species composition or in the physical characteristics of the sea ice (McConville and Wetherbee 1983; Clarke and Ackley 1984).

Above I_{crit}, changes in the photoadaptation index of the epontic cells (I_k) are strongly correlated to underice illumination (I_z) (Fig. 2c, 2f; Table 1). I_z is mainly controlled by air temperature and snow depth (Fig. 2a–2c; Table 1), since the optical properties of sea ice (Grenfell and Maykut 1977; Grenfell 1983) and snow (Grenfell and Maykut 1977) depend on air temperature; ice albedo decreases with increasing ice temperature, and snow albedo decreases with an increase in the proportion of its liquid phase. The increase in I_k at the beginning of May (from ~25 to ~60 μEinst·m^{-2}·s^{-1}) parallels a similar increase in underice illumination (Fig. 2c, 2f), which suggests a

TABLE 3. Mean (standard deviation) nutrient concentrations ($mmol \cdot m^{-3}$) at the five sampling depths (number of observations $N = 11$ (nitrate and phosphate, 10 April to 16 May) and $N = 10$ (ammonia, silicate, and $(NO_3 + NO_2 + NH_4):PO_4$ ratio (mol:mol) 10 April to 13 May)).

	Ice	Ice–water interface	0.5 m	2 m	10 m
NH_4	2.9 (1.7)	2.2 (1.2)	2.5 (1.4)	1.2 (0.7)	0.7 (0.5)
$NO_2 + NO_3$	0.6 (0.4)	2.2 (0.7)	1.9 (0.8)	1.7 (0.6)	2.2 (0.7)
SiO_3	1.9 (0.6)	7.6 (4.7)	14.8 (8.0)	15.3 (8.1)	7.6 (1.6)
PO_4	0.13 (0.15)	0.22 (0.20)	0.31 (0.37)	0.13 (0.08)	0.60 (0.15)
ΣN:P	89.3 (111.0)	25.8 (12.2)	31.9 (38.4)	40.0 (42.5)	5.3 (1.3)

change from shade to light adaptation of the epontic cells. In addition, the fact that $I_k \approx I_z$ indicates a strong photoadaptation of the epontic microflora to the underice light intensities. I_k depends on the light history of the cells (Talling 1957; Steemann-Nielsen et al. 1962; Steemann-Nielsen and Park 1964). Since the ice microflora does not experience the high-frequency light fluctuations that affect the other aquatic microalgae (Legendre and Demers 1984), I_k of the epontic community follows only the seasonal variations in underice light intensity. This change in photoadaptation is accompanied by floristic changes within the epontic community (Fig. 3), some taxa taking advantage of the new light conditions.

Fortnightly Tidal Variations

Aside from seasonal light changes, other environmental factors can influence the photosynthetic activity of epontic microalgae. The inverse relationship (Table 2) between photosynthetic efficiency (α^B) and potential vertical stability of the water column (Richardson number: $R\hat{i}$) suggests an influence on photosynthesis of processes related to the fortnightly tidal variations in water column stability (Fig. 4a, 4c).

Intrusion of brackish water from the plume of the Great Whale River into Manitounuk Sound produces a strong halocline (1- to 2-m-thick upper layer) under the ice (Legendre et al. 1981). During spring tides, vertical upward transport of salt caused by entrainment and/or vertical mixing favors nutrient replenishment of the brackish surface layer (Ingram 1983). This is supported by a positive correlation between salinity and phosphate concentrations ($\tau = 0.45$, $p < 0.001$). Three mechanisms may explain this phenomenon: (1) local tidal mixing, (2) saltwater entrainment across the pycnocline caused by sharp crested internal waves which are more prevalent during spring tides (Turner 1973), and (3) entrainment and mixing processes in the constricted area near Paint Islands (Fig. 1), followed by advection of nutrients towards the sampling station.

Water depth in Manitounuk Sound decreases regularly from 90 m near its entrance to less than 10 m at its inner termination, except near Paint Islands, where a shallow bank abruptly reduces the depth to less than 30 m. Tidal currents in this area are the largest of any region in the Sound. Similar to observations elsewhere, large-amplitude, high-frequency internal waves were generated downstream of the bank during periods of higher than average surface tides (LaFond 1962; Farmer and Smith 1980; Farmer and Freeland 1983). Over the period when large internal waves were observed, mean salinity values in the brackish layer increased continually at our sampling station (Ingram 1983). This response may be explained by either of the last two mechanisms mentioned previously. If tidal mixing is invoked to account for the salinity increase, the most likely site for this to occur is over the Paint Islands bank. Since the mean flow in the brackish layer was into the Sound throughout our sampling period, any water from the lower layer mixed into the brackish layer will be advected in a like manner. Thus, nutrient replenishment of the upper layer would be associated with increasing salinity, which in turn was related to the presence of larger tides.

Several researchers have stated that the epontic microalgae are not nutrient limited (see the introduction). In Manitounuk Sound, the mean ratio of dissolved inorganic nitrogen to phosphorus above the halocline (Table 3) is larger than Redfield's (1934) value of 15. This indicates phosphorus deficiency relative to nitrogen above the halocline, while below (Table 3) the situation is reversed, as previously observed in typical Hudson Bay waters (Legendre and Simard 1979; Pett and Roff 1982). Furthermore, waters under the pycnocline (>2 m) are richer in phosphate than those above (Table 3). The positive relationship between phosphate and salinity, the inverse relationship between phosphate and Richardson number measured five semidiurnal tidal cycles before (Table 2), and the positive relationship between phosphate and α^B (Table 2) all suggest that the lower phosphate and α^B values that follow the neap tides (high $R\hat{i}$ values correspond to high potential vertical stability, Fig. 4) are indicative of phosphate limitation at the ice–water interface.

It is consistent with the partial correlation coefficients (Table 2) to hypothesize that the photosynthetic efficiency (α^B) of the microalgae at the ice–water interface is controlled by vertical mixing, as phosphate becomes depleted in the brackish layer during and following the neap tides (Fig. 4). This hypothesis does not preclude that another nutrient factor, controlled by vertical mixing but not measured in 1982, may be also responsible for the observed variations in α^B. It is well known that nutrient limitation can affect the photosynthetic capacity (P^B_{max}) of microalgae (Thomas and Dodson 1972; Stross et al. 1973; Glover 1980). The data of Falkowski and Stone (1975) suggest that nutrient limitation can also affect α^B, as also reported by Côté and Platt (1983). The time lag in the response of photosynthetic characteristics to environmental changes depends on the growth rate and generation time of the microalgae (Harris et al. 1980). This is consistent with the five semidiurnal tidal cycles observed in Manitounuk Sound, since the generation time of the ice microflora is between 2.5 d (Palmisano and Sullivan 1982) and 6 d (Bunt 1968).

The vertical stability of the water column in Manitounuk Sound is less pronounced in summer than in winter because of a reduced density gradient. However, mean values are of little significance to the processes presently under consideration. Occurrence of small values, indicative of lowered stability, or an alternation between periods of high and low are of greater

concern. The latter combination, resulting from wind effects and fortnightly tidal variability, was used to account for summer phytoplankton variability in Manitounuk Sound (Legendre et al. 1982). For phytoplankton, intermittent summer blooms occurred upon stabilization of the water column following instabilities (Legendre 1981). In winter, alternation of water column stability also plays a major role in the production of microalgae, but in a contrasting manner to that found in summer. Below-average $R\hat{i}$ values under the ice occur during periods of larger tides, when strong velocity shears are found across the pycnocline. Upward salt transport (and associated nutrients) into the brackish layer adjoining the ice occurs during these intervals. Thus, broad peaks of high photosynthetic efficiency at the ice–water interface develop during periods of lowered stability (Fig. 4a, 4c), which is opposite to what is generally observed for phytoplankton. This is explained by the fact that epontic microalgae are permanently growing at a stable interface, where they can use nutrients as they are supplied by replenishment and/or regeneration, while the stable interface for phytoplankton is provided by the vertical stabilization of nutrient replenished water. Epontic microalgae can therefore take advantage of destabilized water column conditions, which is not the case for phytoplankton.

Microalgal Responses to Energy Inputs

Populations of photosynthetic organisms respond to the various forms of energy in their environment. Similar to other ecosystems, the primary source of energy for the epontic microflora is light. Seasonal photosynthesis in Manitounuk Sound does not start before at least 7.6 μEinst$\cdot$m$^{-2}\cdot$s^{-1} diffuse through the ice and snow cover. As in the water column, the use of solar energy varies according to the input of auxiliary mechanical energy (Legendre and Demers 1984). In Manitounuk Sound, microalgal photosynthesis responds to fortnightly inputs of tidal energy that control nutrient limitation at the ice–water energetic interface (ergocline, Legendre and Demers 1985). Photosynthesis of the epontic microflora is therefore governed both by the flux of light through the ice–snow cover and by the fortnightly inputs of tidal energy.

The air–ocean temperature gradient across the ice controls the stability of the ice–water ergocline. In May, the inversion of the temperature gradient, resulting from a sharp increase in air temperature, is followed by a decrease in ice thickness and the washing out of ice microalgae (Fig. 2a, 2e, 2g). The biomass at the ice–water interface is dispersed (Fig. 2e) without significant effects on its photosynthetic efficiency (Fig. 4c). This indicates that the decrease in biomass at the ice–water interface, at the time of ice melting, results from mechanical dispersion and not from physiological stress. After the snow cover has melted (early May, Fig. 2b) the rate of growth of the epontic population thus depends upon the competition between (1) the rate of microalgal production (which is controlled both by solar light transmitted through the ice and nutrient replenishment by tidal energy) and (2) the rate of destruction of the ice–water ergocline by thermal energy.

Destruction of the ice–water ergocline, as a consequence of the inversion of the air–ocean temperature gradient, can be compared to the destruction of the seasonal thermocline by the wind at mid- and high latitudes that follows the inversion of thermal exchanges in the autumn. In all cases, the perturbation or destruction of the ergocline results in lowered biological production. Production of microalgae therefore depends upon three forms of environmental energy: (1) the flux of solar light, (2) the inputs of auxiliary mechanical energy, and (3) the energy exchanges responsible for the maintenance or destruction of ergoclines.

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Effects of Available Dietary Carbohydrate and Water Temperature on the Chronic Toxicity of Waterborne Copper to Rainbow Trout (*Salmo gairdneri*)

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We used a factorial design to determine the effects of dietary carbohydrate content (0.1 or 25.6%) and temperature (10 or 15°C) on the chronic toxicity of waterborne copper (0 or 144 μg $Cu \cdot L^{-1}$) to rainbow trout (*Salmo gairdneri*) over a 12-wk period. Relative to those on the low-carbohydrate (LC) diet, trout reared on the high-carbohydrate (HC) diet developed enlarged, glycogen-filled livers and attained reduced final mean wet body weights. This response was more pronounced at 10 than at 15°C. Whereas Cu exposure had no significant effect on the growth or mortality of either LC or HC fish at 15°C, or LC fish at 10°C, HC fish at 10°C showed significantly reduced final weight and increased mortality. Trends toward reduced liver glycogen and increased serum glucose, characteristic of chronic stress, were apparent in all Cu-exposed fish. In Cu-free water, mean Cu concentrations in liver tissue of HC fish were significantly lower than those in LC fish at both temperatures. Copper exposure resulted in significant increases in liver Cu concentration for all diet treatments except HC at 10°C. Elevated serum sorbitol dehydrogenase levels, indicative of hepatic damage, were apparent in Cu-HC fish at 15°C and in HC, Cu-HC, and Cu-LC fish at 10°C. No treatment effects on either serum protein or hematocrit were evident. The treatments during the growth period affected subsequent lethal tolerance of Cu. While the 96-h Cu LC50 was not significantly altered by diet alone at 15°C, it was elevated in HC fish, relative to LC fish at 10°C. The Cu LC50 of Cu preexposed fish was significantly elevated, relative to parallel groups held in Cu-free water, for LC fish at both 10 and 15°C. This acclimation to Cu was not apparent in HC fish at either temperature: no significant elevation in LC50 occurred as a result of preexposure. We conclude that increased dietary carbohydrate can significantly increase the chronic toxicity of Cu to trout, and that the impact is enhanced by reduced water temperature.

Les auteurs ont utilisé un plan factoriel pour déterminer l'incidence de la teneur alimentaire en hydrates de carbone (0,1 ou 25,6 %) et de la température (10 ou 15°C) sur la toxicité chronique du cuivre hydrique (0 ou 144 μg·L^{-1} de Cu) pour la truite arc-en-ciel (*Salmo gairdneri*) pendant 12 sem. Par rapport aux truites nourries d'aliments pauvres en hydrates de carbone (LC), les truites maintenues à un régime riche en hydrates de carbone (HC) ont subi une dilatation du foie qui s'est rempli de glycogène et elles ont atteint un plus petit poids humide moyen. Cette réaction était plus importante à 10°C qu'à 15°C. Alors que l'exposition au Cu n'avait aucune incidence significative sur la croissance ou la mortalité de poissons LC ou HC gardés à 15°C ou de poissons LC maintenus à 10°C, les individus HC stabulés à 10°C ont présenté une baisse nette du poids final et un accroissement de la mortalité. Chez tous les poissons exposés au Cu, on a noté une tendance vers une réduction du glycogène dans le foie et une augmentation du glucose sérique, caractéristiques de stress chronique. Dans l'eau exempte de Cu, les concentrations moyennes de Cu dans les tissus hépatiques de poissons HC étaient nettement inférieures à celles présentes chez les poissons LC gardés à 10 et 15°C. L'exposition au Cu a entraîné des augmentations importantes des concentrations hépatiques de Cu chez tous les groupes, sauf les HC maintenus à 10°C. Des teneurs élevées en déshydrogénase de sorbitol dans le sérum, indicatrices de lésions au foie, étaient présentes chez les poissons Cu-HC gardés à 15°C et les individus HC, Cu-HC et Cu-LC maintenus à 10°C. Aucune incidence du traitement sur les protéines ou l'hématocrite sériques n'a été décelée. Pendant la période de croissance, les traitements ont influé sur la tolérance ultérieure à des concentrations létales de Cu. La CL50 après 96 h n'était pas nettement changée par le régime à 15°C, mais elle était plus élevée chez les poissons HC par rapport aux individus LC maintenus à 10°C. La CL50 du Cu chez les poissons pré-exposés était nettement élevée, par rapport aux groupes témoins gardés en milieu exempt de Cu, pour les individus LC gardés à 10 et à 15°C. Cette acclimatation au Cu n'était pas évidente chez les poissons HC stabulés à ces deux températures : aucune augmentation significative de la CL50 n'a eu lieu par suite d'une pré-exposition. Les auteurs formulent la conclusion que les hydrates de carbone contenus dans le régime peuvent nettement accroître la toxicité chronique du Cu chez la truite et que cet effet est accru par une faible température de l'eau.

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The nutritional status of an organism can alter the uptake, metabolism, excretion, and hence the impact of toxicants (Boyd and Campbell 1983; Kato 1977). However, little work has been done on the influence of available dietary carbohydrate. In mammals, elevated carbohydrate decreased microsomal oxidation, resulting in increased barbiturate sleeping time in mice and benzylpencillin mortality in rats (Campbell and Hayes 1974).

Rainbow trout (*Salmo gairdneri*) reared on diets high in available carbohydrate develop enlarged, glycogen-filled livers (Bergot 1979; Hilton and Atkinson 1982). This excess liver glycogen was correlated to impaired liver function (Hilton and Dixon 1982). We previously reported (Dixon and Hilton 1981) that increasing the carbohydrate content of the diet fed to rainbow trout during rearing reduced their subsequent lethal tolerance of waterborne copper. Although demonstrating the impact of elevated dietary carbohydrate prior to testing on lethal copper tolerance, that work revealed nothing about the sublethal impact of copper on fish receiving high-carbohydrate diets during exposure. In addition, reduced temperature can decrease the ability of salmonids to utilize carbohydrate (Phillips et al. 1948; NRC 1973). Lower temperatures could presumably increase the detrimental impact of elevated dietary carbohydrate levels on copper tolerance.

The work reported here was carried out to test the null hypothesis that neither the excess liver glycogen resulting from elevated dietary carbohydrate nor reduced water temperature would alter the chronic toxicity of waterborne copper to rainbow trout.

Materials and Methods

We used a factorial design to determine the effects of dietary carbohydrate content and temperature on the chronic toxicity of waterborne copper to rainbow trout. Fish were reared for 12 wk at either 10 or 15°C on one of two diets which varied in the amount of available dietary carbohydrate. They were simultaneously exposed to 0 or 150 $\mu g\ Cu \cdot L^{-1}$. This level of copper exposure (0.35 of the 96-h LC50) was chosen because it represents a moderately chronic state of intoxication (Dixon and Sprague 1981a). The experiment was carried out in triplicate for a total of 24 groups (2 températures × 2 diets × 2 copper concentrations × 3 replicates). Treatment effects were assessed in terms of wet weight gain, liver somatic index (LSI), liver histopathology, liver glycogen and copper content, and serum protein, glucose, and sorbitol dehydrogenase levels. At the end of the growth period, subsamples of fish from each treatment were subjected to bioassays to determine their lethal tolerance of waterborne copper.

Two practical trout diets were formulated (Table 1) to be isonitrogenous and theoretically isocaloric on the basis of the metabolizable energy (ME) values (37.44 $kJ \cdot g\ fat^{-1}$, 16.74 $kJ \cdot g$ digestible $carbohydrate^{-1}$) of Smith (1975). The diets were processed by steam pelleting in a California Pellet Mill (San Francisco, CA). The ash, moisture, and crude protein content of the test diets were determined as described by Horwitz (1980), the lipid content by the method of Bligh and Dyer (1959), and the glucose content as described by Hilton et al. (1982).

Juvenile rainbow trout, obtained from Goossen's Trout Farm, Otterville, Ont., were subdivided into two groups and acclimated to laboratory conditions for 2 wk at either 10 or 15°C. During acclimation they were fed to satiation four times daily with a nutritionally complete commercial diet.

TABLE 1. Formulation and analysis of the test diets fed to rainbow trout during the growth period.

Ingredient	Diet: Low carbohydrate (%)	Diet: High carbohydrate (%)
Capelin meal[a]	43	43
Soybean meal	24	24
Wheat gluten	5	5
Alpha-floc	13	—
Cerelose (D-glucose)	—	25
Salmon oil	12	—
Vitamin premix	2	2
Mineral premix	1	1
Analysis[b]		
Protein	37.2	37.9
Lipid	17.8	6.9
Ash	7.3	8.3
Moisture	7.4	6.2
Glucose	<0.1	25.6

[a]12.5% lipid by analysis.

[b]Based upon the mean of three samples with protein, lipid, ash, and glucose content of the diets expressed on a dry matter basis.

The growth study was initiated by distributing 120 fish to each of 24 rectangular, self-cleaning polyethylene tanks. Each 65-L tank was aerated and received a continuous flow of water at 600 $mL \cdot min^{-1}$. The temperature (mean ± SD) in 12 of the tanks was maintained at 10.4 ± 0.2°C, with the remaining 12 at 15.2 ± 0.1°C. During the study the fish were fed one of the two test diets at a rate of 3% wet weight per day. The fish were fed four times daily.

Mariotte bottles (Leduc 1966) dispensed copper stock solution (prepared from C.P. grade $CuSO_4 \cdot 5H_2O$) into the dilution water streams of the 12 tanks used for copper treatment, to achieve a nominal copper concentration of 150 $\mu g \cdot L^{-1}$. Copper concentrations were monitored by sampling each treated tank every other day. The control tanks were sampled periodically. Samples were acidified to 1% with nitric acid and stored in linear polyethylene bottles. Copper concentrations were determined by flame volatization atomic absorption spectrophotometry (APHA 1976). Over the 12-wk period, copper concentrations (mean ± SD) for individual replicates ranged from 127 ± 31 (N = 42) to 156 ± 40 (N = 42) $\mu g \cdot L^{-1}$. Since analysis of variance demonstrated that there were no significant differences between the mean copper concentrations of the four copper-treatment groups, the grand mean of 144 ± 21 (N = 504) $\mu g \cdot L^{-1}$, representing 96% of nominal, was used as an indicator of overall copper exposure. The copper level in the 12 copper-control tanks never exceeded the 4 $\mu g \cdot L^{-1}$ background level in the dilution water.

During the 12-wk study pH was measured daily in one randomly selected tank, alkalinity and total hardness from one tank biweekly, and dissolved oxygen in two tanks, one from each of the 10 and 15°C treatments, every other day. The characteristics (mean ± SD) were as follows: pH, 7.8 ± 0.1 (N = 93); alkalinity, 297 ± 4 $mg \cdot L^{-1}$ as $CaCO_3$ (N = 21); total hardness, 448 ± 11 $mg \cdot L^{-1}$ as $CaCO_3$ (N = 21); dissolved oxygen at 10°C, 9.2 ± 0.1 $mg \cdot L^{-1}$ (N = 51) (92% saturation); and dissolved oxygen at 15°C, 8.5 ± 0.1 $mg \cdot L^{-1}$ (N = 48)

(91% saturation). During both the growth period and the subsequent bioassays the photoperiod was 12 h light : 12 h dark.

The number of fish and the total biomass in each of the 18 replicates were measured weekly to determine growth and number of mortalities and to adjust the feeding rate. After 6 wk, 10 fish from each of the eight treatments were killed and individually weighed. The livers were excised and weighed for determination of LSI ((liver weight/body weight) × 100). A sample of each liver was frozen in liquid nitrogen and stored at −20°C for measurement of liver glycogen (Murat and Serfaty 1974). The remainder was fixed in buffered formalin and examined for histopathology by Dr. B. Hicks, Department of Pathology, Ontario Veterinary College, University of Guelph.

After 12 wk, 10 fish from each of the eight treatments were anesthetized with tricaine methanesulfonate (MS 222, Syndel Laboratories, Vancouver, B.C.) and blood was taken from the caudal artery of each fish with a 10-mL plastic syringe fitted with a 20-gauge needle. Blood was transferred to a glass centrifuge tube, held on ice for 30 min to permit clotting, and centrifuged at 8000 rpm for 5 min to isolate serum. The serum was stored in liquid nitrogen until required for analysis of serum protein (biuret method, Sigma Chemical Co., St. Louis, MO), serum glucose (glucose oxidase method, Boehringer-Mannheim Kit, Boehringer-Mannheim, West Germany), and serum sorbitol dehydrogenase (SSDH) (spectrophotometric assay, d'Apollonia and Anderson 1980). Hematocrits were taken for each fish with 40-μL heparinized hematocrit tubes after severing of the caudal peduncle. The fish were killed and the livers removed for determination of LSI and histopathology as outlined above. In addition, samples of liver tissue were frozen for determination of liver copper concentration. Each sample was freeze-dried and the copper concentration determined by flameless atomic absorption spectrophotometry after digestion with nitric and perchloric acids.

In each of the eight lethality bioassays, 10 fish per concentration were exposed to nominal copper concentrations of 0, 270, 410, 610, 940, and 1450 $\mu g \cdot L^{-1}$. Space was available to complete only three bioassays at one time. The 10 ± 0.2°C (N = 21) bioassays with fish from the low-carbohydrate control, low-carbohydrate copper, and high-carbohydrate copper groups began 84 d after the start of the growth study, followed by the high-carbohydrate control group at 88 d. The temperature in the bioassay system was then raised to 15.1 ± 0.1°C (N = 18) and the bioassay with the low-carbohydrate control, low-carbohydrate copper, and high-carbohydrate copper fish initiated on day 93, followed by the high-carbohydrate control fish on day 97. The fish were not fed during the bioassays, which continued for 96 h. Mortality observations were recorded on a logarithmic time series (Sprague 1973) and wet weights at death were determined for all fish.

The bioassay apparatus consisted of an 18-tank system, with each 50-L self-cleaning glass aquarium receiving a continuous flow of test solution at 500 $mL \cdot min^{-1}$ for a 95% molecular replacement time of 4 h (Sprague 1973). Toxicant solutions of appropriate concentration were delivered to each tank by a "Chadwick" diluter (Weinstein 1978). Mean copper concentrations, determined by daily sampling of each tank as outlined above, ranged from 81 to 93% of nominal with coefficients of variation ≤7.3%. Holding conditions did not differ significantly from those outlined above for the growth study.

Effects on wet weight gain were determined by regressing $\log_{10}$ of mean weight on time for each of the 24 replicates and comparing the slopes of the regression lines by factorial analysis of variance (Steel and Torrie 1960). In addition, mean wet weights for each replicate at 0, 6, and 12 wk were compared by analysis of variance and Tukey's comparison of means (Steel and Torrie 1960). Both methods gave the same result. Results for mortality, liver glycogen, LSI, hematocrit, liver copper concentrations, serum protein, serum glucose, and SSDH were analyzed by factorial analysis of variance and, where applicable, differences were determined by Tukey's comparison of means. LC50s were calculated by probit analysis (Finney 1971) using mortalities and mean assayed copper concentrations. Since no control mortalities occurred, correction was not necessary. The 96-h LC50s were compared on the basis of relative potency (Finney 1971). Prior to analysis the data were tested for normality (D'Agostino's D test, Zar 1974) and homogeneity of variance (Bartlett's test, Zar 1974). All data were found to be normally distributed. When nonhomogeneity was encountered, appropriate transformations were made before analysis. The nontransformed data are, however, presented here. With the exception of relative potency calculations which were done manually, all data were analyzed with standard SAS programs from the library of the Department of Computing Services, University of Waterloo. The statistical significance of results was assessed at the 0.05 probability level.

Results

The mortality rate of 9.2% for fish held at 10°C on the high-carbohydrate diet and exposed to copper for 12 wk was significantly higher than the rates for all other treatments, which ranged from 1.7 to 3.6% and were not significantly different from each other (Table 2). The majority of mortalities (93%) occurred during the first 6 wk of the study.

Mean wet weight was altered by temperature, diet, and copper exposure during the growth period (Table 2). After both 6 and 12 wk the mean wet weights of the treatment groups held at 10°C were significantly elevated relative to their counterparts at 15°C. At 6 wk, in those 15°C groups receiving no copper exposure, the mean wet weight of fish fed the high-carbohydrate diet was significantly reduced relative to those on the low-carbohydrate diet. Although copper exposure had no effect on the weight of fish fed the low-carbohydrate diet, it resulted in a significant reduction for those fed the high-carbohydrate diet. The results at 10°C paralleled those at 15°C: reduced weight as a result of elevated dietary carbohydrate and a significant copper effect on high-carbohydrate, but not low-carbohydrate, groups.

After 12 wk on the treatments the significant trends were the same as those outlined above, with one exception. Whereas a 6-wk copper exposure had caused a significant reduction for high-carbohydrate fish at both 10 and 15°C, at 12 wk a copper effect on high-carbohydrate fish was apparent only at 10°C.

After 6 wk at both 10 and 15°C in copper-free water, fish fed the high-carbohydrate diet showed LSI and liver glycogen levels that were significantly elevated relative to those fish fed the low-carbohydrate diet (Table 3). There was no significant interaction between temperature and the size of the increase. Within diets, copper exposure resulted in a significant reduction in LSI and liver glycogen at 15°C, but no effect at 10°C.

After 12 wk the significantly different trends in LSI between treatments were the same as those at 6 wk, with the exception that temperature was now also found to have an effect on fish held in copper-free water. For both diets the LSI at 10°C was significantly reduced relative to that at 15°C.

For fish held in copper-free water during the 12-wk study,

TABLE 2. Wet weights and mortalities shown by rainbow trout during the growth period. Values are means (SD) of the three replicate measurements for each treatment. Weight was determined as biomass divided by the number of fish for each replicate. Mortality was determined as the total % mortality over the growth period for each replicate. Within each column, values without a superscript letter in common are significantly different.

Dietary carbohydrate content	Temperature (°C)	Copper concentration ($\mu g \cdot L^{-1}$)	Weight at 0 wk (g)	Weight at 6 wk (g)	Weight at 12 wk (g)	Mortality (%)
Low	10	0	2.3 (0.3)[a]	8.6 (0.5)[a]	15.1 (1.4)[a]	1.7 (0.9)[a]
High	10	0	2.6 (0.3)[a]	6.9 (0.4)[b]	9.9 (0.6)[b]	2.9 (1.8)[a]
Low	10	144	2.4 (0.2)[a]	8.4 (0.4)[a]	14.8 (1.1)[a]	3.1 (1.3)[a]
High	10	144	2.5 (0.2)[a]	5.2 (0.2)[c]	7.2 (0.3)[c]	9.2 (1.1)[b]
Low	15	0	2.3 (0.3)[a]	10.1 (0.5)[d]	19.2 (1.3)[d]	2.6 (1.4)[a]
High	15	0	2.5 (0.3)[a]	7.3 (0.4)[b]	15.9 (0.2)[a]	2.1 (1.6)[a]
Low	15	144	2.5 (0.2)[a]	9.9 (0.5)[d]	19.3 (1.4)[d]	2.8 (1.6)[a]
High	15	144	2.7 (0.3)[a]	6.1 (0.3)[e]	16.2 (0.8)[a]	3.6 (1.4)[a]

TABLE 3. Liver somatic index (LSI), liver glycogen content, and liver copper concentration of rainbow trout during the growth period. Values are means (SD) with a sample size of 10. Those without a superscript letter in common are significantly different.

Dietary carbohydrate content	Temperature (°C)	Copper concentration ($\mu g \cdot L^{-1}$)	LSI		Liver glycogen at 6 wk (%)	Liver Cu at 12 wk ($\mu g \cdot g^{-1}$)
			6 wk	12 wk		
Low	10	0	1.55 (0.09)[a]	1.49 (0.07)[a]	4.60 (1.04)[a]	143 (31)[a]
High	10	0	2.11 (0.21)[b]	2.53 (0.22)[b]	9.37 (1.29)[b]	62 (19)[b]
Low	10	144	1.39 (0.11)[a]	1.30 (0.13)[ac]	3.55 (1.26)[ac]	429 (62)[c]
High	10	144	1.83 (0.20)[b]	2.10 (0.20)[bd]	8.97 (2.35)[b]	94 (17)[b]
Low	15	0	1.35 (0.15)[a]	1.25 (0.11)[ce]	4.33 (0.99)[a]	162 (30)[a]
High	15	0	1.88 (0.18)[b]	1.91 (0.17)[d]	7.54 (1.56)[b]	88 (21)[b]
Low	15	144	0.98 (0.12)[c]	0.93 (0.09)[f]	2.57 (0.53)[c]	390 (53)[c]
High	15	144	1.39 (0.14)[a]	1.45 (0.14)[ae]	5.38 (1.24)[a]	241 (38)[d]

mean liver copper concentrations in fish fed the high-carbohydrate diet were significantly reduced relative to those fed the low-carbohydrate diet (Table 3). No temperature interaction was evident. Copper exposure at 15°C resulted in significant increases in copper concentrations for both high- and low-carbohydrate fish. While the same was true for low-carbohydrate fish at 10°C, no increase was apparent for those fed the high-carbohydrate diet.

Histopathological examination revealed that the livers of fish fed the high-carbohydrate diet consistently had a higher degree of vacuolation than those of fish on the low-carbohydrate diet. The contents of the vacuoles were Periodic Acid Schiff positive, indicating an intracytoplasmic accumulation of glycogen. No other lesions were evident.

Neither copper exposure nor diet had a significant impact on serum glucose levels at 15°C (Table 4). At 10°C, however, whereas diet alone had no effect, copper-exposed fish fed the high-carbohydrate diet showed significantly elevated levels relative to all other groups.

Serum sorbitol dehydrogenase (SSDH) levels at 15°C were not affected by diet composition alone (Table 4). Copper exposure had no impact on low-carbohydrate fish, but caused a significant increase in SSDH levels in high-carbohydrate fish. In copper-free water at 10°C, SSDH levels were elevated in high-carbohydrate fish relative to low-carbohydrate fish. Copper exposure resulted in a significant SSDH increase in fish fed the low-carbohydrate diet, but no further increase in the already high level of those fed the high-carbohydrate diet. No significant differences in either serum protein or hematocrit were noted.

Diet, temperature, and copper exposure during the growth period altered the subsequent lethal tolerance of fish to copper (Table 5). At 15°C, diet alone had no effect on the 96-h copper LC50 shown by rainbow trout. Copper-exposed fish on the low-carbohydrate diet showed an LC50 of 748 $\mu g \cdot L^{-1}$, significantly higher than the value of 462 obtained with low-carbohydrate fish previously held in copper-free water. With fish held on the high-carbohydrate diet, copper preexposure had no effect on LC50 values: 310 $\mu g \cdot L^{-1}$ for control versus 383 $\mu g \cdot L^{-1}$ for preexposed fish. The trends at 10°C were the same as those above with one addition. For fish previously held in copper-free water the low-carbohydrate LC50 of 550 $\mu g \cdot L^{-1}$ was significantly higher than the value of 341 $\mu g \cdot L^{-1}$ obtained with high-carbohydrate fish.

Discussion

Relative to those fed the low-carbohydrate diet, fish fed the high-carbohydrate diet in copper-free water had enlarged, glycogen-filled livers and reduced final wet weight. As would be expected (Hilton and Slinger 1981), all fish showed reduced growth at 10°C relative to those at 15°C. The carbohydrate impact was more pronounced at the lower temperature. Compared with the low-carbohydrate fish, the mean wet weight of

TABLE 4. Serum glucose, protein, and sorbitol dehydrogenase (SDH) levels and hematocrits shown by rainbow trout at the end of the 12-wk growth period. Values are means (SD) with a sample size of 10. Those without a superscript letter in common are significantly different. SDH is expressed as micro-international units (μU) where 1 international unit equals the amount of enzyme that will convent 1 μmol substrate·min^{-1} at 25°C.

Dietary carbohydrate content	Temperature (°C)	Copper concentration (μg·L^{-1})	Serum glucose (mg·100 mL^{-1})	Serum protein (mg·mL^{-1})	SDH (μU·mg serum protein^{-1})	Hematocrit (%)
Low	10	0	70 (16)^{a}	55 (20)^{a}	173 (29)^{a}	36.5 (4.1)^{a}
High	10	0	104 (21)^{ac}	39 (12)^{a}	492 (96)^{b}	34.2 (3.2)^{a}
Low	10	144	88 (23)^{a}	51 (17)^{a}	326 (46)^{c}	33.6 (3.6)^{a}
High	10	144	142 (17)^{b}	56 (19)^{a}	496 (107)^{b}	29.5 (4.1)^{a}
Low	15	0	88 (19)^{ac}	46 (24)^{a}	261 (82)^{acd}	35.2 (3.8)^{a}
High	15	0	97 (21)^{ac}	31 (18)^{a}	248 (43)^{cd}	36.1 (3.4)^{a}
Low	15	144	119 (19)^{bc}	52 (20)^{a}	206 (32)^{ad}	34.3 (3.1)^{a}
High	15	144	124 (17)^{bc}	40 (12)^{a}	488 (112)^{b}	36.5 (4.0)^{a}

TABLE 5. Copper tolerances and mean (SD) (N = 60) post-bioassay wet weights shown by rainbow trout subjected to the various treatments during the growth period. For the 96-h LC50s, values without a superscript letter in common are significantly different.

Dietary carbohydrate content	Temperature (°C)	Copper preexposure concentration (μg·L^{-1})	96-h LC50 (μg·Cu L^{-1})	95% fiducial limits (μg·Cu L^{-1})	Weight (g)
Low	10	0	550^{cb}	446–638	16.3 (2.5)
High	10	0	341^{a}	269–447	10.8 (1.1)
Low	10	144	995^{d}	865–1170	15.1 (2.1)
High	10	144	403^{ab}	322–507	8.4 (0.9)
Low	15	0	462^{ab}	360–587	20.3 (3.1)
High	15	0	310^{a}	251–384	16.8 (2.1)
Low	15	144	748^{cd}	590–920	21.6 (3.0)
High	15	144	383^{ab}	314–478	16.5 (2.3)

high-carbohydrate fish at 12 wk was reduced by 35% at 10°C versus 17% at 15°C. While all groups showed elevated LSI at 10°C, relative to those at 15°C, the carbohydrate-induced increase in LSI was also enhanced by low temperature: 70% at 10°C versus 35% at 15°C with a parallel trend in liver glycogen level. It is evident that low temperature resulted in decreased carbohydrate utilization as evidenced by decreased growth performance and increased LSI.

Both water temperature and carbohydrate interacted to enhance copper toxicity during the growth period. The level of copper exposure used, 144 μg·L^{-1}, is a level to which trout can acclimate with respect to growth (Lett et al. 1976; Waiwood and Beamish 1978; Dixon and Sprague 1981a). This trend was apparent in low-carbohydrate fish at 15°C: at both 6 and 12 wk there was no difference in weight between control and exposed fish. High-carbohydrate fish at 15°C showed reduced mean wet weight at 6 wk, but by 12 wk acclimation had occurred: no copper effect on growth was apparent. At 10°C there was no copper effect on growth in low-carbohydrate fish at either 6 or 12 wk. Conversely, the mean wet weights of the copper-exposed, high-carbohydrate fish were significantly reduced, relative to high-carbohydrate controls, at both 6 and 12 wk. This enhanced toxicity of copper and inability to acclimate was further substantiated by the incidence of mortality. The only treatment group that suffered significant mortality was the high-carbohydrate copper group at 10°C.

Further evidence for the interactive effect of temperature and available dietary carbohydrate on chronic copper toxicity was apparent from the blood and liver measurements. Copper toxicity acts as a classic stressor in salmonids, increasing the mobilization of liver glycogen reserves with a concurrent increase in serum glucose levels (Donaldson 1981; Wedemeyer and McLeay 1981). This pattern was observed for both high- and low-carbohydrate fish exposed to copper at 15°C; significant decreases in both LSI and liver glycogen relative to copper-free fish were obtained for both groups. Trends towards increased serum glucose were also apparent, although not statistically significant. While no meaningful reduction in LSI or liver glycogen resulted from copper exposure at 10°C, serum glucose levels were elevated, significantly so in high-carbohydrate fish. This tends to indicate that at 10°C the glycogen loading of the liver by dietary carbohydrate was compensating for the copper-stressor mediated mobilization of glycogen to the serum glucose pool. Elevated serum glucose may also be indicative of reduced glucose utilization, further verifying the increased impact of dietary carbohydrate at 10°C.

Copper residues in liver tissue were significantly higher in fish fed the low-carbohydrate diet relative to those fed the high-carbohydrate diet, at both 10 and 15°C. This indicates a specific, although as yet unexplained, copper–glycogen interaction in hepatic tissue. Copper exposure at 15°C increased liver copper concentration in both high- and low-carbohydrate fish,

moreso in low-carbohydrate fish. This response is characteristic of copper exposure (Dixon and Hilton 1981) and reflects the normal metabolism of copper. This increase in liver copper with copper exposure was also evident in low-carbohydrate fish at 10°C. Conversely, exposure of high-carbohydrate fish resulted in no significant increase in liver copper levels. High carbohydrate and water temperature were interacting to alter hepatic copper metabolism. The level of copper accumulated in hepatic tissue is directly correlated to copper tolerance (Dixon and Hilton 1981), and increased liver glycogen can impair liver function (Hilton and Dixon 1982). Tanaka (1982) reported that carbon tetrachloride-induced liver damage can significantly reduce both cadmium and metallothionein levels in the liver of cadmium-exposed rats. Probably the impact of a high level of dietary carbohydrate, enhanced by low temperature, resulted in increased liver glycogen with a reduced ability to withstand copper toxicity.

The concept of carbohydrate-induced liver damage is reinforced by the observed SSDH levels. Increased levels of the hepatic enzyme SDH in serum have been correlated to liver damage and can be used as a method of quantifying liver damage in salmonids (D. G. Dixon, unpubl. data). In the 15°C portion of this study, SSDH was significantly elevated only in copper-exposed high-carbohydrate fish. Low and high carbohydrate alone and low carbohydrate with copper exposure had no impact. At 10°C the only treatment that did not elevate SSDH was low carbohydrate in copper-free water. All other groups showed significantly elevated SSDH values, indicating liver damage. The pattern of SSDH elevation among treatments could indicate a direct copper–carbohydrate interaction, one that is enhanced at 10°C. No clear explanation is currently available.

At the end of the growth period the lethal tolerance to copper of the fish that had been subjected to the various treatments was altered by temperature, copper preexposure, and diet. Copper LC50s at 10°C were all slightly elevated relative to their 15°C counterparts. Relative to those grown on low-carbohydrate diets, fish on high-carbohydrate diets were less tolerant of acute copper exposure, moreso at the lower temperature.

Fish that were preexposed to copper during the growth period subsequently showed different trends in lethal copper tolerance. Fish preexposed or acclimated to sublethal levels of copper develop enhanced lethal tolerance to copper in the form of an increased incipient lethal level (ILL) (Dixon and Sprague 1981a). This tolerance is thought to result, at least in part, from the production of hepatic metallohionein which exerts a protective effect with respect to the toxicity of the metal (Dixon and Sprague 1981b). During this study, copper-preexposed fish reared on the low-carbohydrate diet developed significant tolerance, relative to low-carbohydrate controls; the ILL increased by 62% at 15°C and 81% at 10°C. Fish held on high-carbohydrate diets during copper preexposure did not show this response. No significant increases in ILL occurred, providing further evidence that the elevated dietary carbohydrate level had impaired the ability of the fish to withstand copper toxicity.

In summary, elevated levels of available dietary carbohydrate can increase the chronic toxicity of waterborne copper as evidenced by reduced growth, increased mortality, altered hepatic copper metabolism, and reduced ability to acclimate to copper. In addition, this impact is enhanced by reduced temperature, most likely as a result of the reduced ability to metabolize the dietary carbohydrate.

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REVIEWS/SYNTHÈSES

Microstructure of Fish Otoliths

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Otolith microstructure examination has found an increasing number of applications in recent years. However, few workers have critically assessed the assumptions upon which the age and growth inferences are based or considered the potential for environmental modification of microstructural features. This paper reviews present applications and their assumptions and suggests future directions. Particular attention is given to the premises that the frequency of increment formation is constant and that the width of increments is proportional to fish growth. A hypothesis of increment formation is presented which appears consistent with the numerous and often conflicting studies reported to date. The presence of an endogenous circadian rhythm of increment formation is invoked, entrained by photoperiod, but susceptible to modification by other cyclic environmental variables. Increments formed as a result of the circadian rhythm (once per 24 h) may be induced by different processes than those induced through the action of environmental cues (often > 1 per 24 h), thus explaining apparent morphological differences in increment structure noted by some workers. Temperature fluctuations appear to be a primary source of subdaily increments and are a potential source of error in otolith interpretation.

Au cours des dernières années, on a trouvé un plus grand nombre d'applications à l'examen de la microstructure des otolithes. Toutefois, peu de chercheurs ont fait une évaluation critique des hypothèses sur lesquelles sont bassées les conclusions sur l'âge et la croissance ou ont tenu compte des modifications environnementales potentielles des caractéristiques microstructurales. La présente étude fait le compte rendu des applications actuelles et des hypothèses connexes et propose des orientations futures. On porte une attention particulière aux principes selon lesquels la fréquence de formation de zones de croissance est constante et la largeur des zones est proportionnelle à la croissance du poisson. On présente une hypothèse sur la formation de zones qui semble conforme aux nombreuses études souvent contradictoires réalisées jusqu'à maintenant. On a recours à la présence, pour la formation des zones, d'un rythme circadien endogène qui est régi par la photopériode mais sujet à des modifications sous l'effet d'autres variables environnementales cycliques. Les zones formées selon le rythme circadien (une par 24 h) peuvent être induites par des processus autres que ceux qui sont produits sous l'effet de facteurs environnementaux (souvent, plus d'une par 24 h), ce qui expliquerait les différences morphologiques apparentes dans la structure des zones notée par certains chercheurs. Les variations thermiques semblent être une cause importante de la formation de plusieurs zones de croissance en une journée et représentent une source potentielle d'erreurs dans l'interprétation des otolithes.

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Scales, otoliths, opercular bones, fin rays and vertebrae are examples of structures that are commonly used for age and growth inferences. However, interpretation of age and growth from any bony structure of fish is based on the assumptions that periodic features are formed at a constant frequency, and that the distance between consecutive features such as scale circuli or annuli is proportional to fish growth. These assumptions have been questioned, notably in the case of scale annuli, structures previously assumed to be formed yearly. Blacker (1974) has indicated that both age and genetic factors may influence the rate of production of structures commonly referred to as annuli. In addition, environmental variables such as feeding frequency and photoperiod may affect both the rate of formation and distance between successive scale annuli (Bilton 1974), thus complicating or invalidating age and growth inferences. Moreover, conventional age determination methods have little utility for sub-yearling fishes and tropical species, where seasonal marks such as annuli are not generally present.

The relatively new finding by Pannella (1971) and subsequent workers that many teleost fish deposit otolith growth increments with a 24-h periodicity appeared to offer a method of assessing age and growth with greater accuracy and precision than was previously possible. It also offered a means of age determination for species or life history stages where such data were previously unavailable. Daily growth increments in otoliths of teleost fish are now known to be a widespread phenomenon, present in taxa in both freshwater and marine habitats, and in species distributed from the polar regions to the tropics. In addition, the assumptions of constant frequency of formation and proportionality between otolith and fish growth appear to be well met, perhaps more so than is the case with annuli. In this paper, we critically review the evidence supporting these assumptions.

The terminology of otolith microstructure, in common with that associated with other aspects of age and growth studies, is often rather confused with an abundance of synonymous terms whose definitions are based on subjective criteria. For example, growth increments (the terminology used here) have been called rings, lamellae and growth units to name just a few. Primordia, structures found in the nucleus and thought to be centres of accretion, have been referred to as nuclei, foci and kernels. To avoid such ambiguities, we have adopted a standard set of terms referring to the parts of the otolith and its microstructure (Fig. 1). A growth increment is a bipartite structure, usually formed over 24 h, consisting of incremental and discontinuous zones (terminology of Mugiya et al. 1981). When viewed with a light microscope, the incremental zone appears as a broad, translucent band, while the discontinuous zone is relatively narrow and opaque. When a series of daily growth increments is etched with a weak acid and viewed with a scanning electron microscope (SEM), incremental zones appear as relatively wide, lightly-etched areas while the discontinuous zones are narrow and deeply-etched (Fig. 1).

Incremental otolith growth occurs through differential deposition of calcium carbonate and protein over a 24-h period. Under high magnification ($> 1000\times$), the crystal structure is apparent with the long axis of the crystals oriented perpendicularly to the growth increments. Individual crystals are enmeshed in a proteinaceous matrix, a band of which apparently terminates crystal growth at each end (the discontinuous zone) (Dunkelberger et al. 1980). However, use of the term "discontinuous" is somewhat misleading in that some continuity of the crystalline network is often maintained. The crystalline structure of the lightly etched zone is thought to be largely of calcium carbonate in the aragonite configuration (Mugiya et al. 1981) although vaterite, another mineral form of calcium carbonate, is occasionally present (Carlstrom 1963; Campana 1983a; Brothers 1984). A matrix of the protein otolin (M.W. 150,000), characterized by a high abundance of acidic amino acids, makes up much of the narrow, deeply etched zone (Degens et al. 1969; Dunkelberger et al. 1980; Ross and Pote 1984). The matrix structure is sheet-like, with tightly packed fibers 8 nm in diameter. Ultrastructural details of both the crystalline network and the organic matrix are presented elsewhere (Irie 1960; Degens et al. 1969; Dunkelberger et al. 1980; Watabe et al. 1982; Mann et al. 1983).

While nothing is known of the matrix formation cycle in otoliths, the cyclic nature of calcium deposition has been elucidated by workers using the radioisotope ^{45}Ca. Mugiya (1974) showed that macular cells secreted ^{45}Ca into the endolymphatic fluid surrounding the otoliths. Mugiya et al. (1981) noted that the rate of accretion on various parts of the otolith was proportional to the concentration of adjacent macular cells. They also demonstrated that the rate of calcium deposition on goldfish (*Carassius auratus*) otoliths slowed around sunrise, possibly as a result of reduced macular cell secretion. This circadian rhythm of calcium deposition is almost certainly under endocrinological control (Simkiss 1974; Dacke 1979), yet parallels between scale and otolith growth are difficult to identify. For example, scale growth ceases under conditions of food deprivation, and in cases of severe stress, resorption may occur. Similar phenomena have not yet been documented for otoliths. Otoliths continue to grow under conditions of food deprivation (Marshall and Parker 1982; Campana 1983a; Neilson and Geen 1984), while fish stressed by exertion (Campana 1983b) or by exposure to low pH (Geen et al. 1985) do not show evidence of otolith resorption. Thus, under many circumstances, otoliths provide a more representative growth record than do scales. A further advantage of using otolith microstructure examination for age determination is that otoliths are often the first calcified structures that appear during the early development of teleosts. Otoliths may then have utility for age determination when scales are absent or for species where scale growth is irregular or unpredictable.

That otolith size reflects fish size so closely serves to underscore its utility for growth studies. The conservative nature of otolith growth relative to scale growth may reflect the functions of each: the otoliths as organs of equilibrium and hearing presumably must maintain precise configurations with respect to other parts of the fish's otic apparatus, whereas the scale's function as part of the integument may permit greater latitude in functioning as part of the calcium reserves.

In this paper, we review the existing and potential applications of otolith microstructure examination in the fields of fisheries biology and management. In addition, we critically assess how well otolith growth reflects fish age and growth at the daily level of precision.

Methodology

Microstructural examination of otoliths is a three-stage process consisting of otolith mounting, preparation and observation. Specific techniques vary with the age and size of otolith, increment width and clarity, degree of resolution required, available equipment and application. In this section, we briefly review and contrast the techniques now available.

Of the three pairs of otoliths that occur in teleost fish, the sagittae are usually the largest and most commonly used for microstructure studies. Of the other two pairs of otoliths (the lapilli and asterisci), the former are useful in circumstances where the sagittae are small and comparatively delicate (i.e. in cyprinids), and indeed may be preferred to sagittae in many other species of fish.

All fish otoliths are acellular, mineralized structures. As such, decomposition under relatively dry conditions does not occur over the short term (< 3 yr). Dry storage and/or mounting on standard microscope slides prior to microstructural examination are therefore common practices. Mounting media include instant glue, thermoplastic cement, and liquid media such as Euparal. The use of Permount is not recommended, since it is not rigid enough to allow subsequent grinding. Liquid storage in 95% ethanol is also possible. However, acidic solutions are incompatible with calcareous structures such as otoliths, even at mildly acidic pHs of 6.0–6.5. Therefore, partial otolith dissolu-

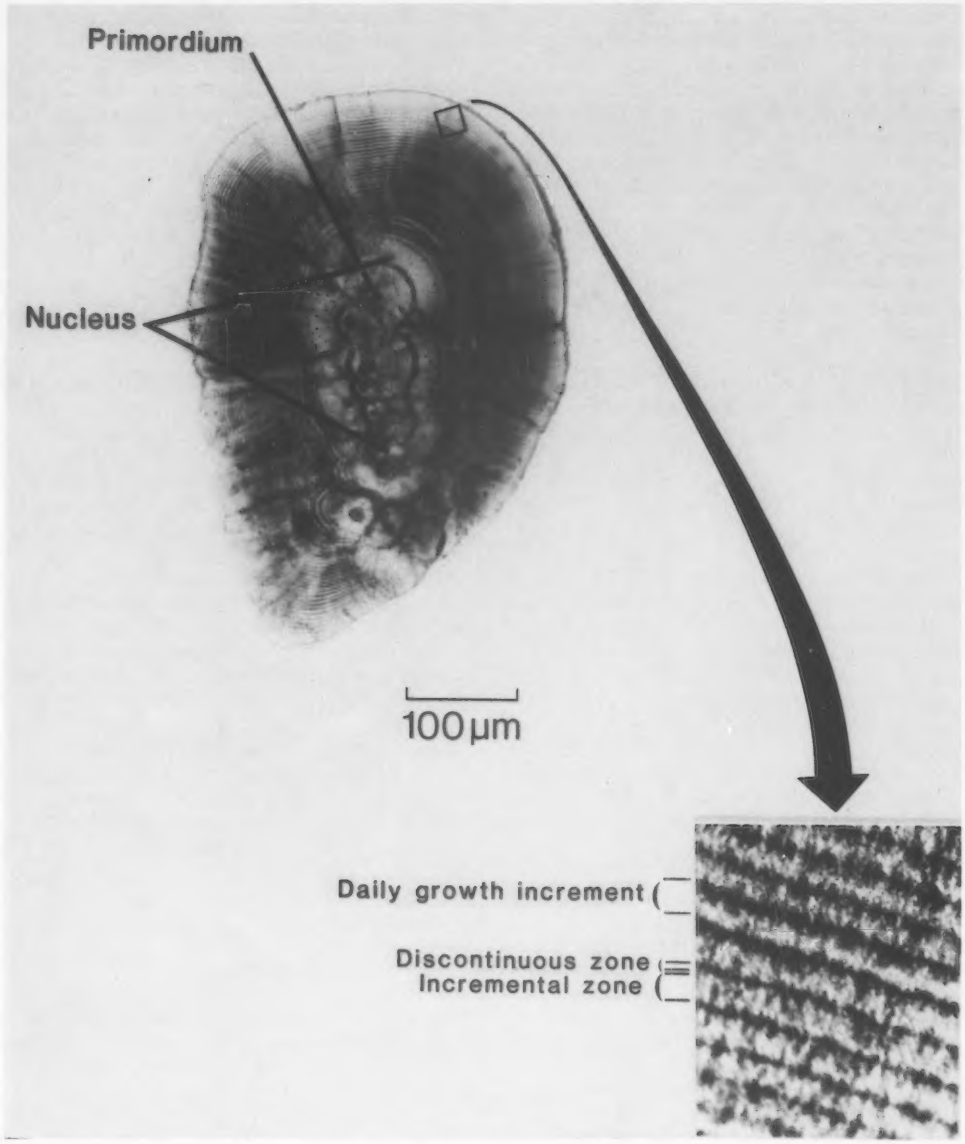

FIG. 1. Incremental growth sequence in a juvenile chinook salmon otolith (sagitta) as viewed with transmitted light. As indicated, the periphery of the nucleus is delimited by the first contiguous increment encircling all central primordia.

tion may be expected of fish/otoliths stored in buffered formalin or solutions containing <70% ethanol (Radtke and Waiwood 1980). Due to surface area to volume considerations, dissolution rates and otolith size are inversely related, rendering larval otoliths most susceptible to acidic degradation.

Where otolith preparation is necessary, its purpose is to enhance the distinction between the incremental and discontinuous zones that comprise each bipartite growth increment. Visual differentiation of adjacent growth increments is only possible because of the difference in light transmission characteristics between each component of a given increment. Therefore, daily increments can be discerned only when viewed as adjacent transverse sections; this necessitates focusing along the midplane of one of the three primary otolith orientations.

Several methods are available for enhancing light microscopic images; all act to reduce refractive effects and increase light transmission through the otolith. Increased transparency of overlying material can be obtained through use of clearing media such as Euparal or immersion oil (Radtke and Dean 1982). However, overclearing cannot always be reversed and will reduce visibility of microstructural features. Sectioning, grinding, polishing, and acid-etching physically remove the calcareous overburden and are frequently used techniques for otolith preparation (Wild and Foreman 1980; Wilson and Larkin

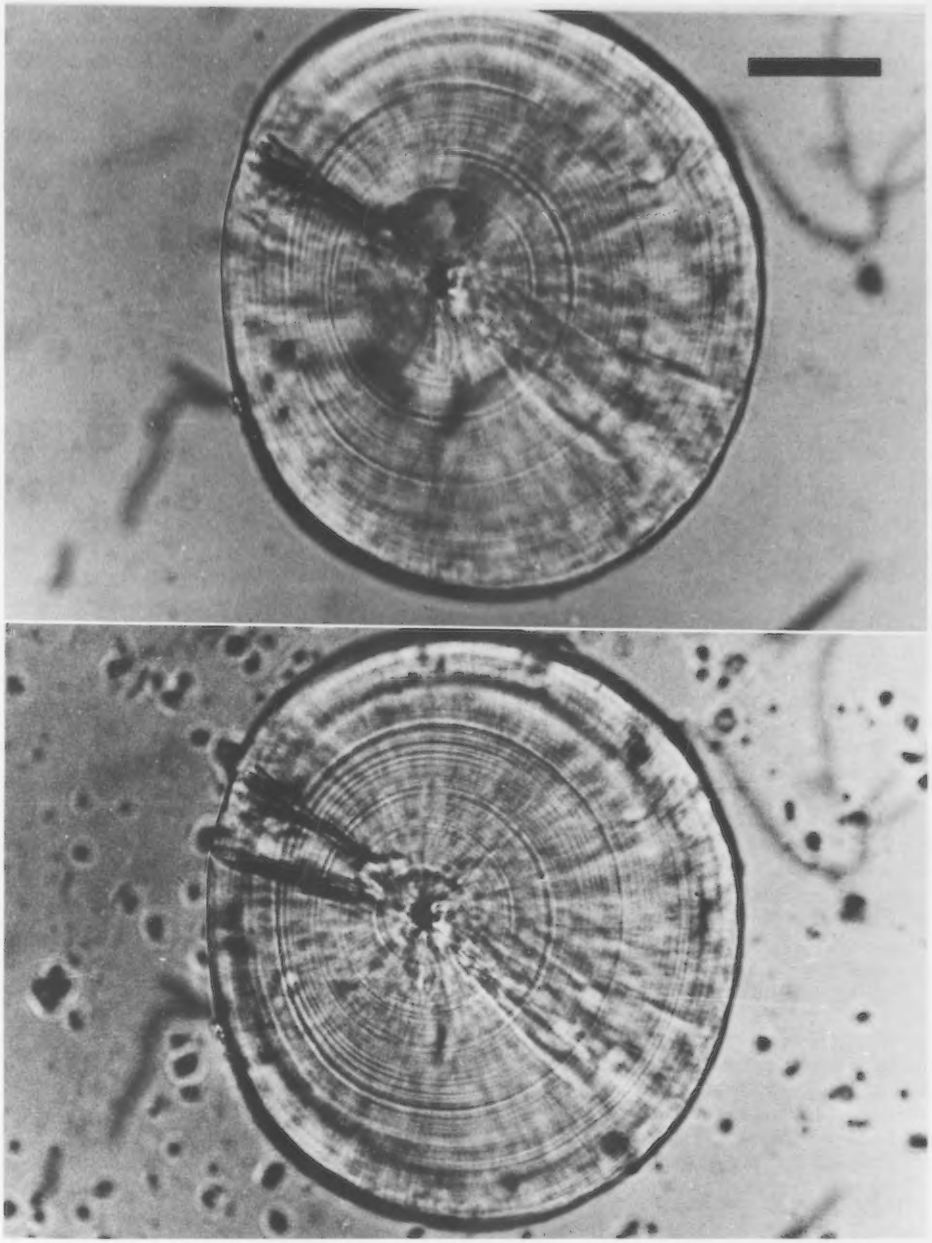

FIG. 2. Comparative photomicrographs of a single wild Atlantic herring otolith before and after preparation for light microscopy. Differences are most apparent in the perinuclear region where the most material was removed during grinding. Top, unground; bottom, ground and polished. Bar = 30 μm.

1980; Campana and Neilson 1982). Overgrinding of otolith edges due to beveling of hand-held preparations can be eliminated through use of grinding jigs that maintain an even grinding plane (Neilson and Geen 1981). Grinding from both sides (to form a thin section) requires more preparation time, but can result in preparations of superior quality (Campana 1984a). Caution must be observed during application of all of these techniques, since they are irreversible and can lead to ruined preparations if carried out past the midplane. Nevertheless, removal of material above the midplane almost invariably improves the resolution of increments observed microscopically, even in the case of translucent larval otoliths (Campana 1984b). Comparative micrographs of ground and unground otoliths from wild herring (*Clupea harengus*) larvae demonstrate the difference that grinding can make, particularly in the perinuclear area (Fig. 2).

Certain techniques in light microscopy can also improve viewer resolution of growth patterns. Use of crossed polarizing filters can be helpful in locating larval fish otoliths both in the initial dissection and on the microscope slide. Microscope–video systems serve to enlarge the image, simplifying subsequent increment counts and measurements. While these systems do not improve resolution, electronic enhancement of contrast is possible.

Whereas otolith preparation for light microscopy is designed to enhance light transmission differences between incremental and discontinuous zones, preparation for SEM and acetate impressions takes advantage of differences in chemical composition between the zones. Both SEM and acetate techniques rely on differential etching to produce contoured surfaces amenable to topographic examination. Contrary to expectation, weak acid solutions such as 1–2% HCl appear to remove material from the proteinaceous zone rather than the calcified area (Pannella 1980a; Mugiya et al. 1981). The initial suggestion of Brothers et al. (1976) that the acid solution removed material from the calcified zone at a greater rate has since been reconsidered (E. B. Brothers, 3 Sunset W., Ithaca, NY 14850, pers. comm.). Although HCl solutions are still widely used for etching (Pannella 1971; Neilson and Geen 1982), calcium chelators such as ethylenedinitrilo tetraacetic acid (EDTA) give better results in some situations (Radtke and Waiwood 1980; Campana 1984b). Regardless of the etching agent used, etching times must be regulated to ensure that specimens are not overetched and microstructural features lost. Etched samples may then be gold coated for SEM (Neilson and Geen 1982) or used as molds in the preparation of acetate impressions (Pannella 1980b). Note that the preparation of acetate impressions is under the same grinding and etching constraints as that of SEM. However, unlike SEM, microstructural detail can be lost during creation of impressions, while visual artifacts and limited resolution can be introduced during the subsequent light microscopic examination.

The advantages and disadvantages of the various otolith examination methodologies are linked to the size, morphology, and features of the otolith to be examined. Light microscopy is a fast and flexible means of observation, where otolith preparation and equipment needs are minimal, and focal lengths can be adjusted to follow the contours of nonplanar increments. Limitations include the need for samples translucent enough to allow light transmission, potential confusion of increments with visual artifacts, and a resolution limit that may not be sufficient to differentiate increments of narrow width. The light transmission constraint requires sufficient grinding to prepare a thin section of the most opaque otolith in the sample. Although some workers have rejected the largest, generally fastest-growing otoliths due to special grinding requirements (Geffen 1983), this practice can introduce a directed bias into later calculations. Light micrographs provide a medium for count and measurement purposes (Wilson and Larkin 1980; Campana and Neilson 1982), but their fixed focal length may introduce more visual artifacts than would have been observed through a light microscope. However, with SEM, resolution exceeds that needed for observation of the most narrow increments known, and visual artifacts do not occur. In addition, counts and measurements can be made from photographs, which generally reduces observer error. Restrictions on SEM use include the need for expensive specialized equipment and more involved sample preparation. Unlike the preparation for light microscopic examination, grinding of otoliths for SEM is a mandatory procedure and must be carried out precisely to the midplane to ensure adequate etching. Therefore, SEM is not appropriate for the observation of otoliths with nonplanar increments. Moreover, etching criteria for otoliths from species such as plaice (*Pleuronectes platessa*) have not yet been fully developed (Blacker 1975), and in others, etching success may vary with location on the otolith. Age-dependent etching times can complicate preparations of extended growth sequences. In addition, the preparation of larval otoliths can require specialized techniques (Campana 1984b).

While a given examination procedure may be preferred in certain situations, light microscopy and SEM will generally produce increment counts of similar accuracy and precision if the increments are of sufficient width (i.e. > 1 μm, see Fig. 4) (Campana 1983a). The benefit of SEM use, with its greater preparation time, comes when narrow increments (< 1 μm) are being viewed or if increment widths are being measured. SEM measurements of increment width require a perpendicular angle between the planar surface of the otolith and the impinging electron beam, either through adjustment of the specimen stage or alteration of the path of the electron beam. In general though, increment width measurements are more precise when digitized from SEM photographs than when measured with a light microscope under conditions of variable focal length. The increased use of image analysis systems (Methot 1981) and drawing tubes (Bolz and Lough 1983) has reduced the magnitude of errors associated with measurements obtained using light microscopy. Use of hand counters and blind-labelled preparations has similarly reduced bias during counting. However, errors derived from misidentification of microstructural features cannot be circumvented through use of one observation technique or another (with the exception of visual artifacts). Structures that can be confused with daily growth increments under a light microscope, such as subdaily increments and some checks, can also be confused when viewed with SEM. Edge effects are another source of error common to both techniques, although causes differ. Under a light microscope, transmitted light is refracted at obtuse angles at the otolith edge due to the curved surface. Increments so affected may appear to be laterally compressed or disappear from view altogether. With an SEM, errors due to edge effects are of similar magnitude, but are due to over- or under-grinding at the point furthest from the grinding focus (nucleus). This problem is most accentuated in larval otoliths (Campana 1984b).

Validation of daily increment formation is a necessary prerequisite to otolith microstructure work of any kind. Substantial errors may be introduced into an analysis if the structures observed are subdaily but not interpreted as such. Validation procedures include the use of known-age fish in the laboratory (Brothers et al. 1976; Neilson and Geen 1982), sequential sampling of a population where age-selective migration/mortality does not occur (Struhsaker and Uchiyama 1976), or the introduction of dated marks onto the otoliths. The latter technique can be applied to fish in either the laboratory or the wild and can use chemical or intrinsic marks. Chemical marking techniques commonly employ oxytetracycline hydrochloride, which is incorporated into growing calcified tissues within a day of application (Wild and Foreman 1980; Campana and Neilson 1982). The incorporated compound is fluorescent under ultraviolet light, accurately marks the date of application, and resists fading during prolonged storage in the dark (up to at least 4 yr, E.B. Brothers, pers. comm.). Administration can be through injection (100 mg/kg fish) (Wild and Foreman 1980; Campana

and Neilson 1982), dietary intake (250 mg/kg fish) (Weber and Ridgway 1967), or branchial uptake (30 min in 0.1% saline/ 0.004% tetracycline) (Neilson and Geen 1984), although incorporation times limit the frequency of sequential marks that can be applied (Kobayashi et al. 1964). Acetazolamide, a carbonic anhydrase, has also been used as a chemical marker, but with questionable success (Mugiya 1977; Ralston and Miyamoto 1983). Chemical markers for SEM use may also be available. Some elements such as strontium act as calcium analogs during crystal formation. Since heavy elements are detectable with the X-ray line scans available on most SEMs, one should be able to associate the daily increment corresponding to the application date with a peak in strontium abundance. Although this technique has apparently been applied to the study of growth increments in squid statoliths (Hurley et al. 1985), we have found that similar marks in fish otoliths could not be resolved with the required definition (J.D. Neilson, unpubl. data).

Dated marks can be placed on otoliths through other than chemical means. By taking advantage of some of the intrinsic growth processes of otoliths, natural or induced temporal markers can be used to validate the frequency of increment formation. For example, hatch checks are prominent features of many otoliths and are often used as benchmarks for increment counts (Marshall and Parker 1982; Neilson and Geen 1982). Since they do not necessarily form on the day of hatching, their age of formation must be independently determined for the species under examination. Artificially induced checks can be formed through imposition of stress on known dates (Pannella 1980a; Campana 1983b; Ralston and Miyamoto 1983), although this is not a recommended procedure in situations where other checks also exist which might confuse later identification. An alternate approach might be that of sudden shifts in growth rate that can result in marked changes in increment width (Mugiya and Muramatsu 1982). The usual example of this type of marking scheme involves the sudden provision of large quantities of food to fish over a period of several days (Struhsaker and Uchiyama 1976; Victor 1982). Again, caution is required of this type of approach, since lag times may exist between the provision of extra food and its subsequent reflection on the otolith (Neilson and Geen 1984). As with the use of chemical markers, preliminary work must include a study of the elapsed time between application and appearance on the otolith.

Incremental Growth of Otoliths

Accurate interpretation of microstructural growth patterns in wild fishes requires knowledge of those factors that may affect the production of one increment per day. Environmental and physiological variables such as photoperiod, temperature, feeding, growth, and an endogenous circadian rhythm may all fluctuate cyclically, and all have the potential to influence otolith deposition. Except in laboratory studies, the history of exposure to such variables will generally be unknown. Since modification of the cycle of daily increment production will introduce an error into the microstructural examination, the accuracy and limits of a given application may be affected by these variables. In the following section, we summarize those details of otolith growth relevant to an understanding of the periodic nature of increment formation. Subsequently, we review the evidence concerning microstructure–environment interactions and present a hypothesis of increment formation that is consistent with much of the published work to date.

If the initiation of otolith growth in fishes parallels that suggested for other vertebrates, it is probable that the otolith begins as one or more partially calcified primordia exocytosed by cells in the inner ear. Nucleation points on the primordia would regulate the axial accretion of calcium carbonate, although some form of control would also stem from the surrounding matrix (Mann et al. 1983). The number of primordia produced is probably reflected in the number visible in the more developed otolith and is presumably under genetic control. Fusion occurs some time before hatch, at least in salmonids (Geffen 1983; Neilson et al. 1984). Once incremental growth has begun, the organic matrix is a likely template for the crystallization of calcium carbonate (Degens et al. 1969; Lowenstam 1981; Ross and Pote 1984). If this is so, either calcium carbonate accretion or otolin matrix formation or both must vary over a diel cycle to account for the bipartite structure of a growth increment (Dunkelberger et al. 1980; Mugiya et al. 1981; Watabe et al. 1982). Diel variations in calcium deposition have been well documented (Mugiya et al. 1981; Mugiya 1984), but matrix formation is not as well understood. Matrix formation is probably a continuous process, although there is evidence for differing amounts between the crystalline and proteinaceous zones (Dunkelberger et al. 1980). However, regardless of which otolith component varies cyclically, the existence of daily increments indicates that one or more of the factors influencing deposition rate must vary on a daily basis. The determination of these factors, and their potential variability, is the focus of concern from an applied point of view.

The influence of photoperiod on increment formation has been documented numerous times, although the results are seemingly contradictory. An influential role for photoperiod was suggested when reversal of the light–dark cycle reversed the order of formation of discontinuous and incremental zones in goldfish (Tanaka et al. 1981). In addition, daily increments were not formed in the otoliths of young *Lepomis* (Taubert and Coble 1977) or *Fundulus* (Radtke and Dean 1982) in the absence of a 24-h light–dark cycle. However, disruption of daily increment production through an abnormal photoperiod has never resulted in a 1:1 correspondence between increment formation and the light cycle (Taubert and Coble 1977; Campana and Neilson 1982; Geffen 1982). Moreover, Brothers (1981) reported that light was of secondary importance to increment formation, while other workers reported no inhibition of daily increment formation under either constant light (Campana and Neilson 1982; Geffen 1982; Neilson and Geen 1982) or dark conditions (Neilson and Geen 1982). Fishes of different ages and species were used in these apparently conflicting studies. Although interspecies differences may also exist, the response of increment formation to photoperiod was age-mediated in at least one species (Campana 1984c).

Temperature is a second environmental variable that may potentially entrain increment formation. There is no evidence that daily increment formation is inhibited under constant temperature conditions high enough to promote growth (Taubert and Coble 1977; Campana and Neilson 1982; Neilson and Geen 1982, 1984; Radtke and Dean 1982; Campana 1984c). Nor does increment number vary between temperature levels (Neilson and Geen 1982; Radtke and Dean 1982), except where low temperature has resulted in cessation of fish growth (Taubert and Coble 1977; Marshall and Parker 1982). However, Geffen (1983) has suggested that both photoperiod and temperature influenced increment number in Atlantic salmon (*Salmo salar*) embryos through proximal effects on metabolic rate. Apparently, increments were not formed on a daily basis under either

normal or abnormal light and temperature regimes, although increment formation rates of both less than and greater than 1 per 24 h were reported. Unfortunately, low sample sizes and possible methodological problems limit the value of Geffen's study. In addition, the results of her first experiment were inconsistent with those of her second (increment deposition rates varied by a factor of two between identical light/temperature treatments). In an analogous study of rainbow trout (*Salmo gairdneri*) embryos, J.D. Neilson (unpubl. data) found only daily increment formation under various temperature regimes.

While fluctuating temperatures do not appear to be necessary for daily increment formation, their presence can disrupt or otherwise influence a circadian cycle of otolith deposition. Although no data were presented, Brothers (1981) was the first to note that nondaily increment formation could be induced by short-term temperature fluctuations. Quantitative substantiation of this hypothesis was provided by Neilson and Geen (1984), who reported that a temperature cycle with a 12-h period resulted in the formation of 2 increments/24 h. Furthermore, Campana (1984c) noted that a daily temperature cycle enhanced the visual contrast between adjacent discontinuous and incremental zones in a growth sequence produced under a 24-h light–dark regime. Clearly, a fluctuating temperature regime has the potential to influence the otolith microstructure of wild fishes.

The effect of feeding cues on otolith deposition is more equivocal than is the response to temperature. Increment number appears to be unaffected by food deprivation, at least when body energy reserves are sufficient to enable limited skeletal growth to occur (Marshall and Parker 1982; Campana 1983a; Neilson and Geen 1984; Volk et al. 1984). Such reserves may not have been available to starved northern anchovy (*Engraulis mordax*) larvae, resulting in the cessation of otolith growth (Methot and Kramer 1979). However, Atlantic cod (*Gadus morhua*) larvae continued to deposit daily growth increments for at least 14 d after hatch, despite the absence of food (S.E. Campana, unpubl. data).

It is unlikely that feeding acts as an entraining factor for increment formation, since changes in feeding time are not correlated with shifts in the time of formation of incremental or discontinuous zones (Tanaka et al. 1981). Yet there is evidence that feeding periodicity is correlated to the frequency of increment production. Young chinook salmon (*Oncorhynchus tshawytscha*) fed more than once per day produced significantly more increments than did those fish fed once daily, although increment number was not directly proportional to feeding frequency (Neilson and Geen 1982, 1984). Although no data were presented, a similar suggestion was made by Pannella (1980a). These results have not been substantiated by other studies where daily increment production was unaffected by multiple daily feedings (Taubert and Coble 1977; Campana 1983a). However, the conflicting results may be more a matter of interpretation than of substance. Using an SEM (with its attendant high degree of resolution), Neilson and Geen (1982, 1984) made no attempt to differentiate between daily and subdaily increments; all increments, both daily and subdaily, were enumerated. Only those increments considered to be daily were included in the results of the other, light-microscopic studies. Since Campana (1983a) noted that the incidence of subdaily increments appeared to increase with feeding frequency, it is probable that multiple feedings do induce formation of new growth increments, although their reduced width and visual prominence may allow their identification as subdaily increments. Note that otolith response to feeding periodicity is not restricted to ultradian cycles. When rainbow trout were fed at 3-d intervals, every third growth structure that resulted was of increased prominence. Similar results were not obtained with starry flounders (*Platichthys stellatus*), suggesting that interspecies differences in otolith response may have been related to metabolic rate (Campana 1983a).

The variables discussed to this point have been considered for their direct influence on cyclical otolith growth. However, these and other factors are also the primary controllers of fish growth. In a 1982 paper, Geffen challenged the current theories of increment formation by suggesting that increment number was a simple function of growth rate in larval turbot (*Scophthalmus maximus*) and herring. Since daily increment formation has not been confirmed in a number of slow-growing larvae reared in the laboratory (Laroche et al. 1982; Lough et al. 1982; Campana 1984b), verification of Geffen's (1982) hypothesis could invalidate many applications of otolith microstructure examination.

There is little doubt that cessation of skeletal growth is associated with reduced or intermittent daily increment production; otolith annulus formation is an example of this phenomenon (Taubert and Coble 1977; Victor and Brothers 1982). Other workers have demonstrated that the "growth rate limitation hypothesis" does not apply above an unknown, low growth rate (Taubert and Coble 1977; Barkman 1978; Radtke and Dean 1982). Validation of daily increment formation in faster growing larval turbot indicates that the growth rate threshold must lie between 0.15 and 0.26 mm/d for that species (Rosenberg and Haugen 1982; Geffen 1982). Since the natural growth rates of a number of temperate, pelagic larvae can be very low (Bolz and Lough 1983; Campana 1984b), Geffen's (1982) hypothesis must be taken seriously. However, an alternate hypothesis for apparent nondaily increment formation is one of limited observer resolution, which can be linked to three factors (Campana 1984b):

(1) Constant temperature — there is no doubt that constant temperatures, such as those found in a laboratory environment, reduce increment contrast and render growth patterns more difficult to see (Campana 1984c; Neilson and Geen 1984). Exposure to diel temperature fluctuations, even if through vertical migration (Fortier and Leggett 1983), would be expected in a natural environment. Growth structures in wild-caught larvae are usually more clear than those observed in laboratory-reared specimens (Laroche et al. 1982; Lough et al. 1982; Campana 1984b).

(2) Otolith preparation — despite their small size and translucency, larval otoliths contain narrow growth increments which can be obscured by overlying material, even when larger increments are clearly visible without otolith grinding (Campana 1984b). In many of those studies not able to verify daily increment formation, otolith preparation was limited or absent (Laroche et al. 1982; Lough et al. 1982; Geffen 1982). In such cases, the absence of grinding may have biased increment counts below the actual number.

(3) Resolving power of light microscopy — due to the diffractive nature of light, objects separated by less than 0.20 μm cannot be resolved (Eastman Kodak Co. 1980). This is the theoretical resolution limit of a light microscope, assuming perfect optics, an objective with a high numerical aperture, ideal sample preparation, and a source of illumination with a relatively short wavelength, i.e. green. Therefore, if otolith growth structures are narrower than this value, they will be underrepresented in an increment count.

Geffen (1982) reported that increment counts in her slow-growth treatments were substantially lower than those expected of daily formation. However, in one of the slow-growth treatments, three of eight larvae were less than 20 mm long after 94 d. Allowing 5 d for yolk-sac absorption (Lough et al. 1982), the otoliths of these larvae would have grown 12–34 μm in 89 d. If daily increments were indeed formed in these otoliths, their mean width should have been 0.13–0.38 μm, a range that drops substantially below the resolving power of any light microscope. Considering the curvilinear nature of the otolith length – fish length relationship (Lough et al. 1982), the last-formed increments would have been wider than this, and the first-formed narrower. Thus, verification of daily increment formation via light microscopy would have been theoretically impossible. Note also that similar calculations, coming to similar conclusions, can be made using the data of other studies reporting nondaily increment formation (Laroche et al. 1982; Lough et al. 1982; Campana 1984b). Although this argument does not reject the "growth rate limitation hypothesis" suggested by Geffen (1982), it does suggest that resolution limitations are a viable explanation of the results reported elsewhere. In all cases, the slowest-growing otoliths would have the greatest number of nonresolvable increments, thus giving the appearance of a correlation between increment number and growth rate. A test of this hypothesis would require SEM examination of larval otoliths, a technique that has not yet been fully developed. However, it is interesting to note that SEM was used to detect narrow daily increments in chinook salmon reared at 5°C (Neilson and Geen 1982), whereas increment formation had apparently stopped at this temperature when assessed by light microscopy (Marshall and Parker 1982).

Despite the number of variables that have been suggested as influencing otolith deposition, we present here a hypothesis of increment formation that is consistent with much of the published work to date. The major concepts in the hypothesis are not novel, yet their synthesis is. Incorporation of interspecific differences was not required. The basic premise of the hypothesis is that daily increment formation is linked to an endocrine-driven, endogenous circadian rhythm. We suggest that this circadian rhythm is entrained at an early age by photoperiod, but that certain environmental variables can "mask" the rhythm. Endocrine secretion displays a circadian periodicity in many animals (Simpson 1978; Jacklet 1981; Menaker and Binkley 1981), and through the intermediary of metabolic rate, ultimately controls most physiological processes, including skeletal deposition (Simpson 1978). Circadian rhythms in general have been documented at several system levels in fishes (Gibson et al. 1978; Eriksson and van Veen 1980; Godin 1981). Since the basic features of endogenous circadian rhythms differ little among taxa, expected features of a piscine rhythm would include free-run capability (continuation of a circadian rhythm in the absence of periodic stimuli) and entrainment to a daily environmental cue (zeitgeber) such as the light–dark cycle or a diel temperature fluctuation (Jacklet 1981; Takahashi and Zatz 1982). During the free-run phase, endogenous rhythms generally drift from a 24-h periodicity; cycles of 21–26 h are common (Jacklet 1981). Entrainment coordinates the drifting rhythm to an appropriate environmental cue, a phenomenon known as phase-shifting the circadian rhythm. However, entrainment to a cue with a periodicity differing by more than 2–4 h from 24 h is generally impossible. An exception would be a cycle with multiple harmonics of 24 h, a phenomenon known as frequency demultiplication (Marler and Hamilton 1966). Only one environmental variable may act as the entraining factor (usually the light–dark cycle), although others may act to mask an endogenous rhythm (Enright 1981). A masking agent does not phase shift the endogenous rhythm or affect the period during free-run. However, it can influence the resultant cycle directly, thus obscuring the effect of the endogenous rhythm and inducing a cycle with a frequency equal to that of the masking agent. This frequency does not have to be daily, or even close to daily. As an example of this phenomenon, consider the entraining effect of a light–dark cycle on the activity pattern of fish in a predator-filled environment. Normally the activity cycle would be circadian. Introduction of particularly high levels of predators at specific hours of the day might curtail activity at these hours, thus inducing noncircadian activity cycles. However, the predators would merely mask the influence of the innate rhythm, and it would once again become apparent upon removal of the predators.

Given the characteristics of an endogenous circadian rhythm, surprisingly few tests of its potential association with cyclic otolith growth have been made. Daily increment formation in the absence of periodic environmental cues is suggestive of free-run, but the possibility of the presence of uncontrolled variables cannot be excluded (Taubert and Coble 1977; Campana and Neilson 1982; Geffen 1982; Marshall and Parker 1982; Neilson and Geen 1982.) Experiments in which abnormally short or long photoperiods were used demonstrate only that photoperiod does not act as a masking agent (Taubert and Coble 1977; Campana and Neilson 1982; Geffen 1982, 1983). However, Tanaka et al. (1981) provide support for the hypothesis that an endogenous circadian rhythm entrained by photoperiod synchronizes daily increment formation. Through SEM examination of goldfish otoliths, they were able to demonstrate that a phase-shifted photoperiod phase-shifted the time of daily increment production. An analogous change in the time of feeding produced no such response. Thus, photoperiod appears to have acted as a zeitgeber for the circadian rhythm.

Evidence is also derived from mammalian studies, where endogenous rhythms often appear after birth. Once present, cycle amplitude tends to increase with time until the rhythm is "mature" (Davis 1981). In experiments with plainfin midshipman (*Porichthys notatus*), Campana (1984c) documented an age-modulated disruption of daily increment formation under constant light conditions. The effect of photoperiod disruption decreased with increasing fish age, as has been noted in both fish (Gibson et al. 1978) and mammalian (Sacher and Duffy 1978; Davis 1981) endogenous rhythms. Due to the developmental maturation of endogenous cycles, acclimation of fish to constant light would be expected to occur more rapidly in juvenile than in larval fish. In fact, such a phenomenon has been observed in midshipman (Campana 1984c). Therefore, this evidence and the study of Tanaka et al. (1981) strongly implicate photoperiod as a zeitgeber for an endogenous circadian rhythm. Moreover, this hypothesis is consistent both with those studies where photoperiod effects were absent (through acclimation and use of older fish) (Campana and Neilson 1982; Neilson and Geen 1982) and those studies where constant light disrupted daily increment formation (since newly hatched, unacclimated fish were used) (Taubert and Coble 1977; Radtke and Dean 1982). Of course, proof of the existence of an endogenous rhythm will probably never be obtained, due to the possible existence of uncontrolled variables in any experimental design.

If photoperiod acts as a zeitgeber, any effects manifested on

otolith deposition by temperature and feeding must be due to masking effects. Temperature masking was indicated by a 1:1 correspondence between temperature fluctuations and growth increments, even in the presence of several cycles per day (Brothers 1981; Neilson and Geen 1984). Reinforcement of an endogenously formed daily increment occurred when temperature reduction occurred at night (Campana 1984c). Similar but weaker effects appear to explain the influence of feeding periodicity. In the case of both variables, masking probably occurs at the level of metabolic rate, since the latter is known to be susceptible to environmental influence (Matty 1978). Probable interactions between metabolic rate and activity may also explain the results reported by Neilson and Geen (1984), where artificially induced activity cycles resulted in the formation of otolith increments of a similar frequency. Metabolic rate in turn controls the differential deposition rates of calcium and protein on the otolith, resulting in the bipartite structure of a daily growth increment. Physiologically, this is consistent with the study of Mugiya et al. (1981) where evidence of a circadian rhythm of calcium uptake in goldfish was presented. Uptake of labelled calcium ceased near dawn each day and was associated with reduced plasma levels of calcium and a concurrent reduction in deposition on the otolith. Since plasma calcium levels are internally regulated (Norris et al. 1963; Simkiss 1974; Nordlie and Whittier 1983), it is likely that masking agents similarly modify calcium uptake and/or deposition. If this is verified, resolution of the controversy concerning the morphological differences between daily and subdaily growth increments may be possible. Our hypothesis predicts that one increment per day should be produced at relatively regular intervals due to the circadian rhythm. Asynchronous temperature or feeding fluctuations would then form increments in addition to the one already expected. Since the latter growth structures may be formed at irregular intervals, and since the degree of calcium uptake inhibition will be a function of the strength of the masking agent, the increments so formed may be irregular in width and contrast. In fact, these are the criteria that are often assessed subjectively to characterize increments as subdaily (Taubert and Coble 1977; Campana and Neilson 1982; Marshall and Parker 1982). Quantification of these criteria has been attempted (Campana 1984c). However, on the basis of our experience, such classifications can sometimes be difficult and imprecise (Campana 1984c). The difference between increments formed as a result of an endogenous rhythm (daily) and those induced through other means (subdaily) appears to be a quantitative and not a qualitative one, despite the difference in the processes ultimately responsible for their formation. Therefore, development of fully reliable distinguishing characteristics may prove to be difficult. However, while it is essential to determine the rate of increment formation for an accurate estimate of age from otolith microstructure, a categorization of increments as daily or subdaily is not an absolute requirement. Of course, an age estimate derived from any microstructural feature is always based on the assumption that the frequency of increment formation does not vary during the period of study. Unfortunately, it is often difficult to assess the validity of this assumption when studies of natural populations are being made and subdaily increments are present. For this reason, differentiation of daily and subdaily increments may be warranted, even if subjective criteria must be used.

There are several experiments that can be done to test key parts of the increment formation hypothesis. One of the best would test for the period drift predicted of free-run. However, observational error would probably be of the same magnitude as the expected drift from a 24-h cycle of increment production. Another experiment could test for phase-shifting of increment formation through phase-shifted circadian temperature fluctuations; if temperature acts as a masking agent, phase-shifted increment production should not occur. Further, masking by a 12-h temperature cycle should result in the formation of two increments every 24 h, with reversion to a daily pattern upon elimination of the cycle. Finally, observation of an endogenous circadian rhythm of otolith protein deposition would substantiate our hypothesis. Further substantiation occurs naturally, since structures similar in appearance to daily increments have been observed in Arctic (Townsend and Shaw 1982), Antarctic (Townsend 1980), and deepsea fishes (Rannou and Thiriot-Quievreux 1975). The absence of diel light and/or temperature cues in these environments is consistent with the presence of an endogenous circadian rhythm in the resident fishes.

Since this hypothesis of increment formation allows for the interaction of environmental variables with an endogenous rhythm, it allows the prediction of the degree to which environmental variation may disrupt the formation of a reliable daily growth sequence in wild fishes. With photoperiod as a zeitgeber, masking effects of light are not possible and nondaily increments cannot be formed under variable light regimes. In lightless environments, a free-running circadian period could occur, but a 2-h drift per day would only introduce an 8% error. The only other potential source of error would be the longer acclimation period of newly hatched fish in the absence of a zeitgeber, resulting in a more confused growth pattern during the first week(s) of life.

As a masking agent, feeding periodicity can introduce subdaily increments into the otolith. Multiple daily feedings occur in many fishes (Keast and Welsh 1968; Grove et al. 1978; and others). However, since feeding-induced increments are often fainter than those resulting from the circadian rhythm (Campana 1983a), their presence should be recognizable.

Temperature fluctuations have the greatest potential for the introduction of subdaily increments into the daily increment sequence. Temperature appears to be a strong masking agent, and increments induced through its action can be as prominent (Neilson and Geen 1984) or more so (Brothers 1981; pers. comm.) than those produced as a result of the circadian rhythm. Midday migrations to colder water can result in the formation of two increments per day, as may occur in intertidal starry flounders migrating seawards on a midday low tide (Campana 1984a). In this case, the midday increment was easily differentiated from the nightly one, but migrations between less similar temperature regimes might have resulted in more confusing growth structures. However, in most environments, temperatures fall at night, thus reinforcing the formation of the daily increment. In such instances, cyclic environmental cues act in an additive fashion to the endogenous rhythm and result in increased increment definition in a natural environment relative to a temperature-controlled laboratory setting. Thus, it would appear that daily increment formation is to be expected in most natural environments. The influence of environments with anomalous temperature regimes, coupled with knowledge of horizontal and vertical movements of fish on a diel basis, is an area for further research.

Increment Width

Given a sequence of growth increments of known periodicity

and a relationship between otolith and fish size, estimation of the fish length corresponding to otolith size at each of the marks should be possible. Indeed, this is the basis for the back-calculation of size at age from both scale and otolith annuli (Bagenal and Tesch 1978; Carlander 1981). Back-calculation could be carried a step further by relating the width of an annual growth zone to the otolith–fish size relationship, thereby determining growth rate at age. This approach is seldom justified, since the date of annulus formation is not well defined and may vary with the size, age, and ambient environment of the fish. Since the date of formation of a daily increment can be well defined, these constraints do not apply to the same degree at the microstructural level. Consequently, one should be able to examine an incremental series to estimate both size at age and the instantaneous growth rate over short time periods — at least on average. Preliminary evidence in support of this hypothesis has been presented both experimentally (Wilson and Larkin 1982; Volk et al. 1984) and through observation (Struhsaker and Uchiyama 1976; Pannella 1980a; Victor 1982). Under an environment promoting regular growth, the influence of various temperature (Neilson and Geen 1982, 1984; Campana 1984a) and ration (Struhsaker and Uchiyama 1976; Volk et al. 1984) regimes was proportional to mean increment width. However, a close correspondence between fish and otolith growth at the daily level has not yet been demonstrated. Since a measure of instantaneous growth rate would be of undisputed value, we review here those factors that are known to influence increment width and its relationship to fish growth and otolith morphology.

Daily increment width must reflect fish growth (either allometrically or isometrically) if the two growth patterns are linked by a smoothly monotonic curve. Therefore, the potential value of increment width measurement as a growth indicator rests solely upon the characteristics of their mutual relationship. Under circumstances where the otolith–fish size relationship is temporarily disrupted, increment width loses its proportionality to fish growth.

Several studies have reported an uncoupling or disruption of the otolith–fish size relationship under suboptimal conditions (Brothers 1981; Neilson and Geen 1982; Marshall and Parker 1982; Campana 1983a, 1984c). In one study, an abnormal photoperiod resulted in noncharacteristic otolith growth relative to fish growth (Campana 1984c). Manipulated photoperiods may not occur naturally, but their influence demonstrates that some environmental variables can induce uncoupling. Continued otolith growth through periods of starvation is well documented, even after cessation of linear fish growth (Brothers 1981; Campana 1983a). Although increment width decreased through the period of food deprivation (Campana 1983a; Neilson and Geen 1984), this phenomenon was probably linked to metabolic rate and may not be evident in fishes of low metabolic rate (Campana 1983a).

The processes responsible for continued otolith growth during starvation are presently unknown. The conservative nature is emphasized by the apparent absence of otolith resorption under stressful conditions (Simkiss 1974; Campana 1983b), despite its occurrence in other parts of the skeletal system (Bilton 1974; Simkiss 1974; Ichii and Mugiya 1983b). Uptake of calcium for subsequent deposition on the otolith occurs via a closely regulated branchial pathway (Simkiss 1974; Mugiya et al. 1981; Campana 1983b); little is taken up from dietary sources (Ichii and Mugiya 1983a). Therefore, there is no direct link between calcium uptake and ration level. After uptake, plasma levels passively regulate calcium deposition rate on the otolith (Mugiya et al. 1981). Nothing is known of the relationship between calcium uptake and growth rate, leaving no a priori reason why there should be a direct correspondence between short-term fish and otolith growth. Considering the gradual shifts in metabolic activity that occur upon food deprivation (Phillips 1969), a gradual response of increment formation is not surprising. Indeed, a number of studies to date suggest that otolith growth represents a running average of fish growth rates, with the length of the "run" inversely proportional to metabolic activity (Struhsaker and Uchiyama 1976; Neilson and Geen 1982, 1984; Campana 1983a, 1984a). In an indirect comparison of increment width as a measure of growth, Wilson and Larkin (1982) noted an inexplicable but significant nonlinearity in their regression. In addition, a lagged response of otolith growth to fish growth may be common (Neilson and Geen 1984; M. J. Bradford, Department of Biological Sciences, Simon Fraser University, pers. comm.)

Several other factors may introduce significant intraspecific variability into the otolith–fish relationship. One such factor is the size of the otolith nucleus, which is in turn regulated by the number and spacing of otolith primordia (Neilson et al. 1984). Primordial numbers and placement vary substantially among species, but are typified by at least two types of patterns: a scattered pattern such as that observed in salmonid otoliths (Fig. 1), and a clustered one, such as that of flounders (Fig. 3). Among the species we have examined, the latter pattern occurs more frequently. Within a given species, the size of the nucleus is environmentally determined, at least in part (Neilson et al. 1984). Thus, nucleus length can vary sufficiently among individuals that the otolith–fish relationship is significantly affected (West 1983; Neilson et al. 1984). This in turn has the potential to affect the accuracy of back-calculated growth rates.

Formation of accessory primordia (referred to as "peripheral nuclei" in Campana 1984b) in the otoliths of juvenile fish may also confuse the interpretation of daily increment width. Through an unknown mechanism, these secondary growth centres develop after metamorphosis in many fish species as foci for further otolith deposition (Brothers 1984; Campana 1984b). While we refer to these foci as accessory primordia, we do so acknowledging the possibility that these structures are not analogous to the primordia found in the nucleus. The primordia occur asymmetrically around the central nucleus. Since the size of the otolith will vary with the location of the primordia, substantial variance can be introduced into the otolith–fish size relationship. More importantly, individual growth increments may encircle both primordial types, but with substantially different widths around each (Campana 1984b) (Fig. 3). Therefore, increment widths measured in two different fields on the same otolith will not necessarily be comparable.

Check Formation

Checks, or discontinuities, are characteristic of most otolith growth sequences, where they may record periods of perturbation or stress to the fish. Checks may occur at apparently random locations in the growth record, or delimit incremental patterns of weekly or fortnightly periodicity (Pannella 1971, 1980a; Campana 1984a). In both cases, check location can be associated with a date of formation by enumerating the daily increments between the check and the otolith periphery (date of sampling). Use of this technique has demonstrated that nonperiodic check formation is generally associated with periods of stress or sexual

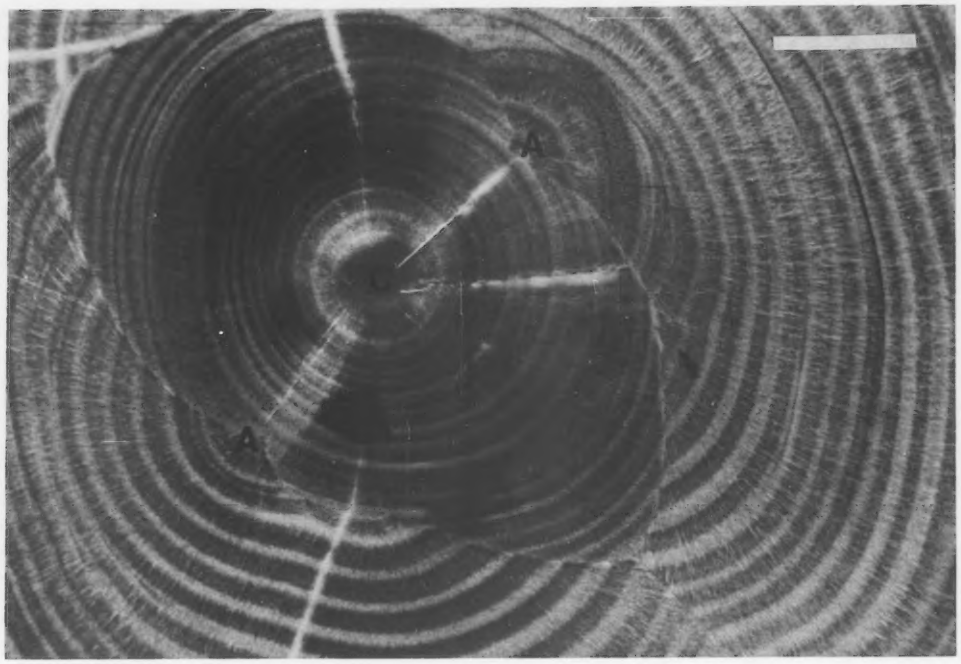

FIG. 3. Central (C) and accessory (A) primordia in the sagitta of a wild, juvenile starry flounder. Note the change in width of a given daily increment as it passes from one field to another. Bar = 50 μm.

maturity (Pannella 1980a; Campana 1983b), while periodic series may be linked to the lunar cycle (Pannella 1980a; Campana 1984a). Since a check may represent a growth interruption of unknown duration, their ubiquity may prove to be a significant problem in the accurate interpretation of a growth sequence. However, the association of some checks with stressful events also suggests their potential utility in defining the size and age at which life history transitions occur. Moreover, dated marks, useful in validation studies, may be formed on otoliths through population-wide stress phenomena such as storms. However, little is known of the physiological processes responsible for check formation despite substantial variance in their visual prominence.

Transmission of light through checks differs relative to other microstructural features, resulting in structures that are immediately distinguishable from surrounding increments. Under SEM, checks appear more deeply etched than surrounding discontinuous zones (Fig. 4). The enhanced visibility suggests that some aspect of otolith deposition has been disrupted. Since otolith growth occurs through cyclic deposition of calcium carbonate and protein, anomalous incorporation of one or both of these components may occur during check formation. Experiments in which young coho salmon (*Oncorhynchus kisutch*) were stressed while immersed in ^{45}Ca water demonstrated that check formation was associated with reduced calcium deposition on the otolith, although concurrent protein deposition was not monitored (Campana 1983b). These results may explain why check prominence can vary with the level of stress experienced. If the reduction in otolith calcium deposition is proportional to stress level, then the calcium:protein ratio will be reduced accordingly in the corresponding growth increment. It is the difference in the ratio between the two components of a bipartite growth increment that accounts for its visual identity. Specifically, the discontinuous zone consists primarily of a proteinaceous matrix, while the incremental zone has a higher calcium content (Dunkelberger et al. 1980; Mugiya et al. 1981). Enhancement of these bipartite composition differences should have a parallel effect on visual prominence. This process describes that suggested to occur during formation of a stress-induced check. However, stress experiments through which calcium and protein deposition were concurrently monitored during check formation have not yet been conducted. Therefore, it is not known if protein incorporation is also reduced through periods of stress. Moreover, quantification of the relationship between check prominence and level of stress has not yet been attempted.

Although consistent with the experimental results, the above hypothesis does not account for some of the observed check characteristics. Otolith growth interruptions may occur regionally: either they may not encircle the nucleus (Campana 1984a), or they may occur in only one of the otolith pair (E.B. Brothers, pers. comm.). Either situation suggests an interruption of otolith growth at the local level. More puzzling are observations of discontinuities that intersect other growth increments (Pannella 1980a; Campana 1984a). Although only present in some taxa, the resemblence of these structures to fault zones (in a geological sense) may be more than coincidental. Refraction of light through the interface between two regions of different refractive indices might result in an unusually prominent structure that we interpret as a check (E.B. Brothers, pers. comm.). However, there is no evidence that such is the case, nor mechanisms to suggest why the interface should be present. An alternate hypothesis was presented by Pannella (1980a), who suggested that checks may demarcate regions of otolith resorption. Resorp-

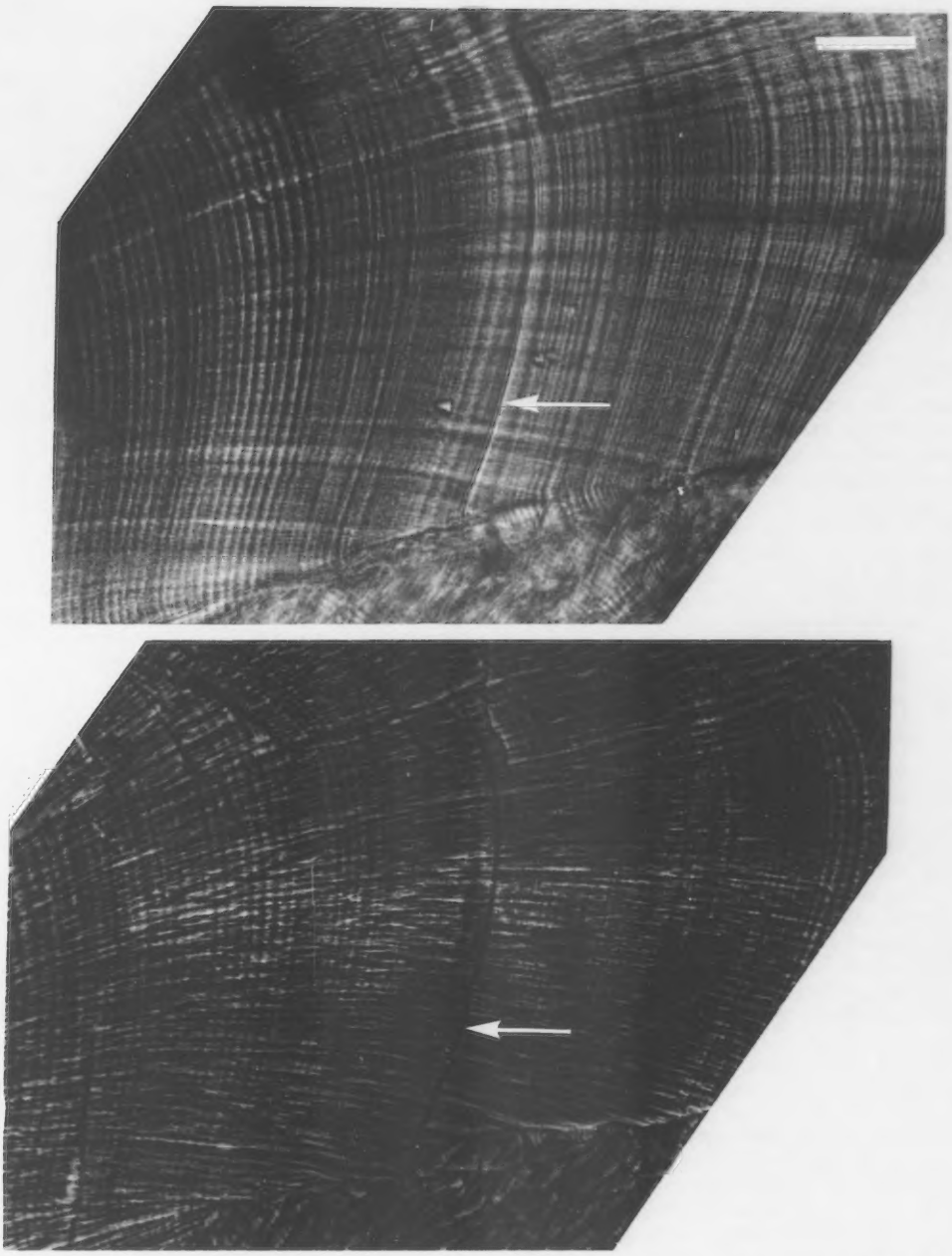

FIG. 4. A check, or growth interruption (indicated by arrow), in a lapillus of the cyprinid *Couesius plumbeus*. Top, viewed with a light microscope; bottom, viewed with a SEM. Bar = 30 μm.

tion could account for some of the characteristics of checks, but the limited experiments performed to date indicate that otolith deposition cannot be reversed (Simkiss 1974; Campana 1983b; Ichii and Mugiya 1983b). We conclude that stress-induced checks represent regions of reduced or interrupted otolith growth and that interregional differences in check prominence may occur.

Stress checks may represent isolated periods of perturbation to individual fish, or a population-wide process recorded on the otoliths of all of the fish. Large-scale stress factors such as storms may disrupt incremental growth in an entire population of bivalves (Kennish 1980), although they are less likely to do so in the case of mobile fish. However, physiologically derived stress can be a nearly universal phenomenon, even though the resultant check is a function of age, not of date. For example, hatch checks are formed in many species of fish and are often

used as benchmarks from which increment counts are made (Marshall and Parker 1982; Neilson and Geen 1982). Presumably, hatching or an associated event is a physiologically stressful period in a fish's life. Hatch checks formed on other than the day of hatching may reflect interspecies differences in the timing of physiologically stressful events (Balon 1984). The presence (Wilson and Larkin 1980) or absence (Brothers and McFarland 1981; Campana 1984b) of checks at other life history transitions may be a function of the physiological stress experienced during the transition, although no studies have been conducted in this area.

Discontinuities need not be induced by stress. Perhaps as a result of localized otolith growth interruptions, check frequency increases as a function of age, particularly in sexually mature fish. Spawning is one potential source of these checks (Pannella 1971, 1974, 1980a). In addition, check formation in marine fish otoliths has been linked to the lunar cycle (Pannella 1971, 1974, 1980a; Campana 1984a). Through an unknown process, starry flounder otolith growth was interrupted at 1- or 2-week intervals in synchrony with the phases of the moon (Campana 1984a). Although the lunar cycle induces a 2-wk period in the tidal cycle, weekly periods are generally not evident. Therefore, the weekly frequency of check formation could not be explained. Checks formed at 2-wk intervals have been used in age determination studies (Rosenberg 1982), but are generally considered to be too variable for this purpose (Campana 1984a; E.B. Brothers pers. comm.).

Present Applications of Microstructure Examination

Age Determination

As we noted earlier, the rate of formation of otolith growth increments theoretically permits age determination with high precision, often to the daily level. Such studies are perhaps the most obvious application of microstructure examination. Accordingly, most workers have reported results related to this aspect of microstructure research. However, as was shown in the previous section, the apparent rate of increment formation may vary, thus causing difficulty in the interpretation of age from otolith microstructure. Few studies have provided validation of the frequency of formation of increments. Indeed, the results of many studies carry the explicit assumption that the otolith increments were formed daily. Studies that have presented data allowing the precise determination of the rate of formation have usually relied on the use of fish of known age (Neilson and Geen 1982; Wilson and Larkin 1982) or on the incorporation of time markers (Wild and Foreman 1980; Campana and Neilson 1982; Neilson and Geen 1984) which allow the interpretation of periodicity of otolith growth from a dated reference, as discussed earlier. A compilation of workers who have conducted studies of the frequency of increment formation is given in Table 1. The number of studies where no confirmation of the frequency of increment formation was provided or where they were assumed to be daily greatly exceeds the number of studies shown in Table 1.

In addition to providing a means for determining ages to the daily level of precision, growth increments have utility for age determination at coarser levels of precision. For example, some workers have used growth increments to corroborate the occurrence of annuli (Pannella 1971; Taubert and Tranquilli 1982; Victor and Brothers 1982). Pannella (1971) noted that daily growth increments were present throughout the first 3–4 yr of life in the red hake (*Urophycis chuss*) and were compressed in the region corresponding to winter growth. Victor and Brothers (1982) used a similar approach to determine the location of the first annulus in a temperate cyprinid. However, the utility of otolith microstructure in such instances may be limited, as discrete growth increments often become unclear after about 200 d (Brothers 1979). Nevertheless, Brothers noted that in some tropical species, recognizable growth increments may persist over the first 2 or 3 years of life. Ralston and Miyamoto (1983) used a rigorous approach to describe the growth of the Hawaiian snapper (*Pristipomoides filamentosus*) entailing the use of otolith microstructure, tetracycline validation techniques, and modal analyses and concluded that otolith growth adequately represented fish growth when time was measured on a scale of years. In general, however, we feel that the utility of otolith microstructure examination for age determination to the annual level of precision is questionable beyond the first year of life, particularly in species found in temperate zones. Growth increments are often so compressed during the winter slow-

TABLE 1. List of studies reporting the frequency of otolith increment formation, including those where a non-daily frequency of formation was observed.

Reference[a]	Species
Pannella 1971	*Urophycis chuss*
Struhsaker and Uchiyama 1976	*Stolephorus purpureus*
Brothers et al. 1976	*Engraulis mordax*
	Leuresthes tenuis
Taubert and Coble 1977	*Tilapia mossambica*
	Lepomis gibbosus
	L. cyanellus
	L. macrochirus
Barkman 1978	*Menidia menidia*
Radtke and Waiwood 1980	*Gadus morhua*
Wilson and Larkin 1980	*Oncorhynchus nerka*
Wild and Foreman 1980	*Thunnus albacares*
	Katsuwonus pelamis
Mugiya et al. 1981	*Carassius auratus*
Tanaka et al. 1981	*Tilapia nilotica*
Bailey 1982	*Merluccius productus*
Campana and Neilson 1982	*Platichthys stellatus*
Geffen 1982, 1983	*Clupea harengus*
	Salmo salar
Neilson and Geen 1982	*O. tshawytscha*
Laroche et al. 1982	*Parophrys vetulus*
Radtke and Dean 1982	*Fundulus heteroclitus*
Rosenberg and Haugen 1982	*Scophthalmus maximus*
Tsuji and Aoyama 1982, 1984	*Pagrus major*
	Engraulis japonica
Victor 1982	*Thalassoma bifasciatum*
	Halichoeres bivittatus
Victor and Brothers 1982	*Semotilus corporalis*
Ralston and Miyamoto 1983	*Pristopomoides filamentosus*
Campana (1983a, 1983b, 1984c	*Salmo gairdneri*
	Oncorhynchus kisutch
	Porichthys notatus
Crecco et al. 1983	*Alosa sapidissima*
Williams and Clarke, 1983	*Herklotsichthys quadrimaculatus*
Radtke 1983, 1984	*Euthynnus pelamis*
	Mugil cephalus
Volk et al. 1984	*Oncorhynchus keta*

[a]If more than one worker has studied the frequency of increment formation in a given species, the first published work is listed

growth period that the identification of discrete increments is difficult.

At an intermediate level of age precision, Pannella (1971) has indicated that patterns of fortnightly frequency were apparent in the red hake otoliths he examined. The fortnightly patterns were attributed to lunar influences, expressed through tidal influences (Pannella 1980a). Such patterns usually consisted of a cluster of six or seven thin daily increments followed by a group of six to eight thick increments. Conceivably, where such sequences recur on a regular basis, they may have utility for age determination. Rosenberg (1982) used counts of fortnightly growth increments to estimate the size at age of young English sole (*Parophrys vetulus*) in Oregon estuaries. However, Brothers (1979) noted that the appearance of lunar patterns is often irregular and difficult to demonstrate critically. Campana (1984a) noted that lunar cycles of otolith growth (expressed through increment width and contrast when viewed with a light microscope) were correlated with tidally modulated variables, particularly temperature.

Among the problems associated with using growth increment counts for age determination, the occurrence of checks, or growth interruptions, is one of the most serious. Thus, examination of otolith microstructure for age determination is less useful in older fish, as intermittent otolith growth leading to check formation may cause difficulties (Brothers et al. 1976; Ralston and Miyamoto 1983).

Just as otolith growth interruptions such as spawning checks can introduce errors into age determinations based on annuli counts, subdaily increments may be incorrectly interpreted as daily growth increments. In addition, narrow increments may be overlooked, particularly in studies using light microscopy. Distinction of daily growth increments from subdaily increments is usually on the basis of subjective criteria such as increment width or appearance (Taubert and Coble 1977; Marshall and Parker 1982; Campana 1984c). However, as was mentioned earlier, differentiation is often difficult and probably represents a significant source of error in some species (Campana and Neilson 1982). Since the variance of counts due to misinterpretation is cumulative, heterogeneity of variance may result when regressions of increment counts on fish age are calculated. The extent of the problem is probably species-specific and related to fish age. However, use of one of the several methods currently available for validation of age estimates removes some of the uncertainty regarding the presence of subdaily increments.

A final source of error is that associated with the date of formation of the first increment. The date of first increment formation may vary from before hatching as with chinook salmon (Neilson and Geen 1982) to the time of first feeding as in anchovies (Brothers et al. 1976). In the absence of data on the age of first increment production, some workers have assumed that it commenced at the onset of an event of biological significance in the fish's life history. For example, Wilson and Larkin (1980) assumed that increment formation in sockeye salmon (*Oncorhynchus nerka*) commenced at the time of emergence of the alevins. However, subsequent studies (Neilson and Geen 1982; Marshall and Parker 1982) have shown that increment formation commenced considerably before hatching. The seemingly erroneous assumption by Wilson and Larkin (1980) was probably responsible for the poor correspondence between observed and expected increment counts, particularly in young fish.

Growth Rate Estimation

Increment widths can provide important information on the day to day growth of fishes (Brothers 1981). In fact, some of the first workers in this field have recognized the potential of otolith microstructure for detailed studies of growth. As noted by Volk et al. (1984), more conventional means of estimating fish growth, such as mark–recapture experiments, suffer from drawbacks which include possible tagging effects on growth, the need to mark large numbers to ensure significant returns, possible size-related mortality between marking and recapture of fish and the requirement for relatively long periods between marking and recapture. However, only recently have researchers taken advantage of the potential of otolith microstructure in that regard. The difficulty in obtaining precise measurements of features that are often <2 μm wide may account for the relatively few detailed studies of growth to date.

To circumvent the problem of measuring individual increments, many authors have chosen to measure the change in otolith radius or diameter as a proxy variable for fish growth (Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Marshall and Parker 1982; Wilson and Larkin 1982, and others). Ralston and Miyamoto (1983) noted that authors using such otolith measurements have not discussed the limitations of the method. With these studies, average daily growth rates were reported. While measurements of otolith radius or diameter are readily obtained, the potential value of discrete increment width data as precise indicators of daily growth is reduced in proportion to the number of increments that comprise the measurement of otolith growth. An alternate approach for studying fish growth entails the plotting of fish size versus increment counts. Many workers have employed this technique for studying relative growth rates of fish obtained from different habitats or environmental conditions (Kendall and Gordon 1981; Volk et al. 1984). Methot (1981) measured the outer three daily increments of larval fishes as indicators of recent growth. However, as shown earlier, such an approach is sensitive to the effects of a lagged response in the relationship between fish growth and otolith growth.

Studies where increment width data are related to the growth of individual fish represent a more powerful application of otolith microstructure examination. Geen et al. (1985) used otoliths from individually branded chinook salmon fry to study short-term growth responses to various pH regimes. However, even in this instance, average increment widths were used and the data smoothed by use of running means. Potentially, the most revealing studies of fish growth from otolith microstructure are those where daily growth of individual fish is compared with the widths of corresponding growth increments. However, we are not aware of any such work. The paucity of such studies may be related in part to the difficulty in obtaining short-term growth data for individual fish as well as precise increment width data, where use of an SEM is often desirable or even necessary.

Due to the lack of detailed studies of the relationship between increment width and fish growth on a daily basis, various workers hold somewhat equivocal views of how closely increment width reflects fish growth at the daily level of precision. Among the more obvious factors that could complicate the interpretation of growth from otolith microstructure are the occurrence of checks or growth increments that are formed at an unknown rate. As noted by Marshall and Parker (1982), Cam-

pana (1983a) and Neilson and Geen (1984), otolith growth may continue under conditions of food deprivation. M.J. Bradford (pers. comm.) has noted that the response of otolith growth to changing ration in chinook salmon fry is not instantaneous. Thus, there is evidence that the widths of growth increments are not necessarily proportional to instantaneous growth rates on the dates in question.

The choice of radius along which increment widths are measured is significant. Because otoliths are not perfectly circular objects, it is not possible to select any one radius that intersects all increments at 90°. To circumvent the problem, relatively short sequences of increments should be selected for width measurements. Alternatively, a perpendicular line may be drawn from each point of intersection of the radius and the increments to allow width measurements in a consistent fashion. Asymmetry of otolith growth along the depth axis, the third dimension, may also cause difficulty in increment width measurements. Correction for curvature in that dimension is difficult and we are unaware of any studies that have quantified or corrected for such error.

Other sources of intraspecific variation in the otolith–fish length relationships are age-related. A curvilinear (or allometric) otolith length–fish length relationship is characteristic of many species during the larval phase (Methot 1981; Laroche et al. 1982; Lough et al. 1982; Campana 1984b), while a linear (isometric) relationship is usual for juveniles (Messieh 1975; Rosenberg 1982; Campana 1984b). Unless the size at metamorphosis is known, back-calculations of growth from juvenile to larva generally cannot be done. Campana (1984b) has documented that in starry flounder larvae, increasing increment widths were better correlated with increasing age rather than increased growth rate, at least before the larvae reached metamorphosis. Crecco et al. (1983) found that growth of larval American shad (*Alosa sapidissima*) as inferred from increment counts and length data, decreased as they approached metamorphosis. However, increment width data were not available in this instance to assess whether otolith microstructure continued to reflect fish growth.

We conclude that the use of increment widths as indicators of instantaneous fish growth rate must be done with caution, unless conducted under rigorous laboratory control or when the calculations are averaged over several days or weeks. Further research on factors influencing otolith deposition and its relation to fish growth would be valuable to further assess the utility of this application of otolith microstructure examination.

Detection of Life History Transition

Several authors have used changes in increment width to indicate transitions in the life history of fish, usually the movement of fish from one habitat to another. Movements from freshwater to an estuarine environment, for example, might be associated with a different water temperature or feeding regime. Such changes might be reflected in the otolith microstructure and would be expected in some species on the basis of laboratory experiments where temperature and feeding regimes were varied (Neilson and Geen 1982, 1984). Neilson et al. (1984) used changes in otolith increment width and appearance to identify the time at which juvenile chinook salmon entered an estuary. Campana (1984b) has used changes in increment width to detect the point of metamorphosis in a series of growth increments from otoliths of starry flounders.

Growth interruptions or changes in increment appearance such as contrast (when viewed with a light microscope) may also have utility for detection of life history transitions. For example, Brothers et al. (1983) estimated the duration of larval life in 12 families of Australian reef fishes by identifying, through subjective examination of various species-specific criteria, the point on the otolith corresponding to when the larvae settled. However, the authors noted that the transitions were often difficult to detect and could only be resolved when they were at least three or four increments from the otolith periphery. In contrast, Victor (1982) apparently had little difficulty in detecting a settling mark on the otoliths of bluehead wrasse (*Thalassoma bifasciatum*). Brothers and McFarland (1981) interpreted stepwise transitions in increment width and the presence or absence of subdaily increments as representing five different life history stages in juvenile French grunts (*Haemulon flavolineatum*). In papers by Brothers and Thresher (1985) and Thresher and Brothers (1985) the hypothesis that prolonged larval life is correlated with broad geographic distribution was tested using examination of growth increments formed during the pelagic life of Indo-Pacific coral-reef fish. In such studies, the timing of initiation of growth increment formation is a possible source of error. If increment production does not commence with the onset of pelagic life then the estimates of the duration of pelagic phase will be in error.

A preliminary study (J.D. Neilson, unpubl. data) of the transition between pelagic and demersal life history stages of Scotian Shelf gadoids did not detect the presence of a transition or settling mark as noted in tropical forms. The absence of a check may reflect the fact that the transition to the demersal life-style apparently does not occur abruptly (P. A. Koeller and J. D. Neilson, unpubl. data).

Checks associated with hatching have been used as reference points from which counts or measurements of increments have been made (Neilson and Geen 1982). While this is an appropriate procedure for species where there is reason to believe that significant stress or other factors associated with hatching might somehow be reflected in the otolith microstructure, there is some indication that for certain species, hatching may be a physiologically insignificant event (Balon 1984). In such cases, a distinct check may not be apparent such as was found in chinook salmon otoliths (Neilson and Geen 1982).

It is worthwhile to note that life history transition studies based on otolith microstructure are subject to the same constraints as are other applications of microstructure examination. Indeed, it may be necessary to conduct separate experiments to determine the rate of increment formation and relationship with fish growth at each stage of a fish's life history.

Estimates of Recruitment and Mortality

Healey (1982) was able to demonstrate size-selective mortality through examination of distributions of scale circulus spacing. As scale circulus spacing is proportional to fish growth, examination of the successive distributions of circuli spacing as the cohort ages may be used to demonstrate the occurrence of size-selective mortality. Scale circuli are analogous structures to otolith increments, but are not formed at as great or as constant a rate. Therefore, there is potential advantage in using otolith increment examination to provide the age-structured data necessary for such studies. Neilson (1984) applied a similar methodology based on an examination of increment widths to demonstrate the possibility of size-selective mortality during the early ocean life of chinook salmon. Crecco et al. (1983) used ages determined from the otolith microstruc-

ture of American shad to determine survivorship curves and mortality estimates. Rosenberg and Haugen (1982) examined individual growth trajectories of larval turbot obtained from back-calculation using otolith growth increments and were able to show that slower growing individuals died at a greater rate. West (1983) located emergence checks on otoliths of sockeye salmon and developed a relationship between otolith nucleus dimension (defined by the extent of the emergence check) and fish length. He then examined frequency distributions of the nucleus measurements in successive samples of the cohort and was able to identify when the selective mortality occurred. However, due to the nature of such analyses, it is not possible to assess the extent of total mortality, only whether size-selective mortality exists. Methot (1982) used otolith microstructure examination to determine the birthdate distribution (defined as the date of yolk absorption) of larval northern anchovy. These data allowed both a comparison of survival between two subsequent year-classes and the determination of intraseasonal patterns of survival.

Use in Taxonomic Studies

Brothers (1984) provided a review of the utility of otolith microstructure examination for systematic ichthyology which was based largely on internal and external morphological characteristics, including the relative sizes and time of formation of the different otoliths. He also speculated on the systematic applications of descriptions of primordia number and type, as well as the value of increment width data and increment appearance in taxonomic studies. Given the variation in microstructural features which are often found in fish of similar age within a species, we feel that the utility of such data for interspecies comparisons might be limited. However, detailed analysis of growth from otolith measurements appears to have promise for stock differentiation. West (1983) found significant stock differences among linear regressions of (ln) fork length versus (ln) total otolith length of emergent sockeye salmon fry from various populations. Conceivably, the measurement of individual increment widths would have revealed the same stock differences. In addition, Uchiyama and Struhsaker (1981) found that on the basis of otolith microstructure, skipjack tuna (*Katsuwonus pelamis*) from the eastern Pacific grew at a slower rate than those from the central Pacific.

Other microstructural features of otoliths appear to have less utility for racial identification. Neilson et al. (1984) reexamined the hypothesis of Rybock et al. (1975) who suggested that otolith nucleus lengths had utility for separating sympatric races of rainbow and steelhead trout. The former authors used microstructural examination to better define the extent of the otolith nucleus. However, in contrast with the findings of the earlier authors, Neilson et al. (1984) were unable to demonstrate significant differences in otolith nucleus length between the two races. In this instance, the exact delineation of the otolith nucleus using microstructural preparation techniques allowed more precise measurements of the nucleus length.

Future Applications of Otolith Microstructure Examination

Many of the applications described in the previous section have not yet reached their full potential. The detailed study of fish growth, for example, has not developed as quickly as anticipated, perhaps due to methodological difficulties. This, in turn, has slowed research on problems such as the relationship between larval fish mortality and subsequent recruitment. However, progress has been made and further developments are expected. There also remain applications of otolith microstructure examination which have received little or no attention from researchers to date. Some of these areas of research are described below.

Despite its pivotal position as a regulator of fish abundance, there are few reliable predictors of year-class success prior to recruitment to the fishery. Both environmental variables and biological processes may influence recruitment, although it is unlikely that either acts in isolation (Lasker 1981). Assessment of the causal processes has been difficult; numerous parameters have been correlated with cohort survival, yet few provide any predictive power (Sissenwine 1984). However, fish growth results from the cumulative influence of both biotic and abiotic factors, and may well be a causal mechanism of year-class strength. Most of the commonly noted correlates of recruitment (temperature, food abundance and predator abundance) have direct influences upon fish growth, which in turn are reflected in the incremental growth sequence in the otolith. Of equal importance is the fact that the growth sequence spans both the larval and juvenile stages of the life history. Thus, no assumptions concerning the "important" ages are necessary. With the determination of size at age and growth rate at age from the otolith microstructure, information can be collected concerning the age at which year class strength is determined. This can be accomplished through collection of independent estimates of cohort size over a range of years, which in turn can be correlated with the growth at age data in the development of a predictive model of recruitment. If such a model was validated, otoliths from prerecruit fish could be examined to estimate the size of the year-class. Although currently feasible, this approach has not yet been pursued. However, less direct applications of otolith microstructure have yielded encouraging results in this field, both through analysis of birth date distributions (Methot 1982) and through determination of mortality rates at age (Crecco et al. 1983).

The identification of spawning locales is another research area in which otolith microstructure examination can be applied. Larvae of a given species, collected over a broad geographic area, can be assigned ages derived from daily increment counts. This information can be integrated with data on regional water circulation patterns to map patterns of larval drift. Given the duration of the egg stage, and approximate current speeds, back-calculated hatch dates can then be used to infer the general area of spawning. Of course, this technique would be most useful for species that spent little time in the egg stage and spawned in discrete locations.

One of the most promising fields to be developed in the future is that of otolith isotope analysis on a spatial scale equivalent to that of a daily growth increment. Previous workers have demonstrated that the ratio of stable oxygen (^{18}O:^{16}O) and carbon (^{13}C:^{12}C) isotopes in whole otoliths of wild fish reflect the ambient temperature in which the fish lived (Devereux 1967; Degens et al. 1969; Mulcahy et al. 1979). Recent laboratory experiments have suggested that physiological processes may alter the predicted isotope ratios, but that a relationship with water temperature does exist (Radtke 1984). Furthermore, studies with fish and other aquatic organisms have indicated that increasing nitrogen isotope (^{15}N:^{14}N) ratios in bone are correlated with increasing trophic levels (Schoeninger and DeNiro 1984). Given the fact that otolith material is apparently not

recycled after deposition and that stable isotopes are incorporated in a manner influenced by the ambient environment, it appears likely that isotope analyses of given daily increments would reflect both the ambient temperature and feeding habits of a fish on the dates in question. In other words, this type of analysis could allow the reconstruction of an individual fish's past movements and general feeding habits at a daily level of resolution. Until now, technological constraints have restricted isotope analyses to that of whole otoliths. However, the ion microprobe can be used to determine isotope ratios on a spatial scale of 10–25 μm (Karsten et al. 1982; Exley 1983), which approaches that of short sequences of growth increments. Calibration of the technique with temperature profile data would allow inferences to be made with respect to migration routes and even diel vertical migrations. In conjunction with more standard increment measurements, individual otoliths could be analyzed to provide a daily record of size at age, growth rate at age, life history transitions, ambient temperature, and trophic status. Although such data would be useful in the study of most fishes, otoliths could prove to be the only data source for rare or infrequently sampled species. For example, resolution of the North American eel (*Anguilla rostrata*) – European eel (*A. anguilla*) taxonomic controversy (Williams et al. 1984) may be possible through such an examination.

Stock identification is another field in which otolith microstructure analysis may be valuable. Multivariate analyses of elemental composition are based on the assumptions that ambient elemental concentrations vary by region and are incorporated into tissues with growth. The elemental load at hatch is considered to be one of the few natural tags of wild fish (Lapi and Mulligan 1981). Through elemental analysis of whole fish (Calaprice 1971) and scales (Lapi and Mulligan 1981), a limited form of stock discrimination has been demonstrated. However, in both cases, the structure/fish analyzed was exposed to waterborne elements in areas and at times other than that of hatch. Analysis of the perinuclear region of the otolith would remove this potential source of variance and may increase discriminatory powers. Use of more sophisticated devices such as the ion microprobe would further enhance resolution. A related application would take advantage of the chronological sequence of growth increments and the elements incorporated into each: line scans with an ion microprobe might allow the detection of both specific pollutants and the date on which the fish were first exposed to them.

In summary, the potential of otolith microstructure research illustrated in previous sections remains largely unrealized. Major hindrances to further progress include the question of interpreting the presence of subdaily increments in otoliths from fish populations in natural environments, the poorly understood relationship between increment width and somatic growth, and inadequate methods for preparing otoliths that have a degree of concavity along the sagittal plane (often the case in older fish). In our view, such problems represent the most appropriate subjects for future microstructure research. Once resolved, many of the far-ranging applications proposed thus far may then be feasible.

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NOTES

Evidence of Decreasing Spatial Diversity in British Columbia Salmon Stocks

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Walters, C. J., and P. Cahoon. 1985. Evidence of decreasing spatial diversity in British Columbia salmon stocks. Can. J. Fish. Aquat. Sci. 42: 1033–1037.

Escapement records indicate a severe decline since 1950 in the number of streams contributing significantly to salmon production in southern British Columbia. To account for 90% of the escapement for chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), pink (*O. gorbuscha*), and chum (*O. keta*), one need examine only about half as many streams now as in 1950. The deterioration has been most pronounced for coho; only 40 of 350 south coast streams now account for 80% of the recorded escapement. The apparent changes are due partly to reduced monitoring effort rather than actual stock declines, but deterioration in the monitoring system is itself a cause for major concern.

Les données sur la remonte révèlent un déclin important, depuis 1950, du nombre de cours d'eau contribuant de façon significative à la production salmonicole dans le sud de la Colombie-Britannique. À l'heure actuelle, 90 % de la remonte de saumons quinnat (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), rose (*O. gorbuscha*) et kéta (*O. keta*) peut être observée dans environ la moitié seulement du nombre de cours d'eau par rapport à 1950. Cette détérioration est beaucoup plus prononcée pour le coho ; ainsi, 40 des 350 cours d'eau de la côte sud représentent 80 % de la remonte enregistrée. Ces variations évidentes sont en partie attribuables à un effort de surveillance réduit et non à des baisses réelles du stock ; la dégradation du système de surveillance est cause d'inquiétude importante.

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Pacific salmon are produced in hundreds of spawning streams in British Columbia. Most of these streams cannot be managed separately, and harvests are mainly taken in large mixed fisheries such as the Georgia Strait sport, coast wide troll, and Johnstone Strait net fisheries. Crude indices of escapement levels have recently been assembled from field surveys conducted by fishery officers since 1948 and recorded on so-called BC 16 records. These records are too inaccurate to permit much quantitative analysis, such as stock–recruitment relationships, but even a casual glance at them suggests some alarming, qualitative changes in the spatial distribution of escapements. Many small runs have disappeared since 1950, and even some major stocks have declined substantially. On the other hand, some stocks have increased, and it is difficult to get an intuitive feeling for net change over the period of record.

This note summarizes evidence that spatial structure of the production system is indeed deteriorating, as evidenced by declines in the number of streams contributing significantly to total escapement in southern British Columbia statistical areas 11–27. Escapements have been recorded for approximately 350 streams in these areas, which surround Vancouver Island and the Georgia Strait (excluding the Fraser River and a few streams to the north of it). The data were made available to us in a computer data base by A. Gould, Department of Fisheries and Oceans, Nanaimo, B.C.

A Diversity Measure

For four species (chum, *Oncorhynchus keta*; coho, *O. kisutch*; chinook, *O. tshawytscha*; pink, *O. gorbuscha*), we calculated 6-yr average escapements for each of the area 11–27 streams for the years 1948–83. For years when a stream was not visited, the observed escapement was taken to be zero. Then for each species and 6-yr period, we ranked the streams by average escapement (1 = highest average, 350 = lowest average). The rank orders were not always consistent over time, i.e. a particular stream might rank high in 1948–53 and then low in 1978–83. Larger rivers tended to be higher and relatively more stable in rank than small streams, but this pattern was not completely consistent.

Next we cumulated the average escapements by stream rank order, so rank order 1 was assigned the highest escapement, rank order 2 was assigned the highest and second highest

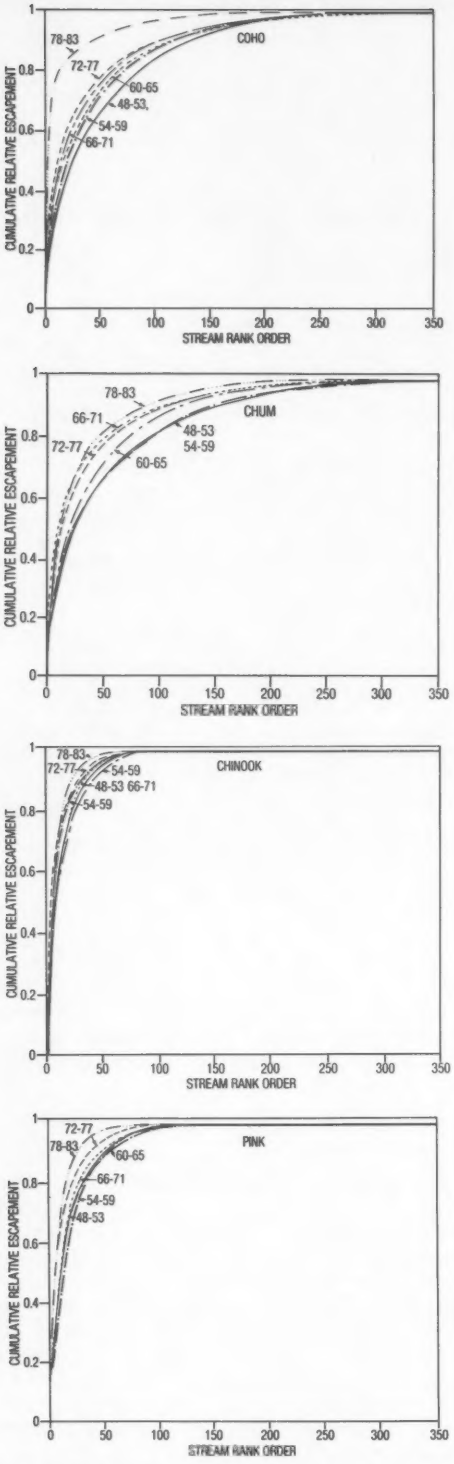

FIG. 1. Cumulative relative escapement as a function of stream rank order for six time periods, British Columbia statistical areas 11–27.

escapements, and so forth. The resulting curve of cumulative escapement versus escapement rank order is a direct diversity measure. Below we shall call this measure the "rank order curve." Similar equitability/heterogeneity measures (Peet 1974) have been widely used in ecology. Economists call it (with axes reversed) the "Lorenz curve" (Lorenz 1905; Taillie 1979) or "concentration curve" and use it to describe distribution of wealth and concentration of industrial activity.

If all streams had equal average escapement, the rank order curve would be a straight line with slope equal to that average, i.e. each stream would add the same amount to cumulative escapement. If all the escapement were concentrated in one or a few streams, the rank order curve would rise very steeply and then plateau sharply, with most streams not adding at all to the cumulative escapement. Temporal decrease in diversity should be reflected by a steepening of the curve over time, that is by movement of the curve away from the straight line representing maximum possible diversity with all streams contributing equally.

To eliminate effects of temporal trends in total escapement, we normalized the rank order curves by dividing each by its maximum (total escapement for the period). This convention also makes it easier to extract qualitative information from the curves, such as the number of streams that would have to be monitored in order to account for 90% of the total escapement.

Results

Normalized rank order curves as defined above are shown in Fig. 1, and temporal trends in overall escapements are shown in Fig. 2. For all four species, it is clear that observed escapements became more concentrated (less spatially diverse) between 1948–53 and 1978–83. Within the limits of the very crude escapement estimates used, it appears that the change has occurred rather smoothly over time. The number of streams needed to account for 80% of total recorded escapement has been cut roughly in half since 1950.

The top ranking 10 streams for each species and period are listed in the Appendix. These listings show that the rank order of dominant streams has remained relatively stable over time, at least in the sense that some streams have consistently been top contributors.

The most striking deterioration has apparently been with coho salmon, for which only 40 (out of 350) streams now account for nearly 80% of the observed escapement. However, field personnel have noted that coho are particularly difficult to enumerate, and that enumeration effort (time spent counting, number of field employees) has fallen in recent years. Also, coho exploitation rates increased during the 1970's, mainly due to growth in the sport fishery (Argue et al. 1983); this change would be expected to hurt some stocks more than others. Another factor is noted in the Appendix: 3 of the top 10 coho escapements for 1978–83 were for stocks that had previously not been major contributors, but were subject to major enhancement projects in the 1970's (Puntledge, Quinsam, Qualicum); these three stocks contributed 29% of the total recorded coho escapement for the 1978–83 period.

Discussion

The changes shown in Fig. 1 may be attributed to a variety of factors, the most obvious being (1) local stock declines due to habitat deterioration, (2) widespread increases in fishing mortal-

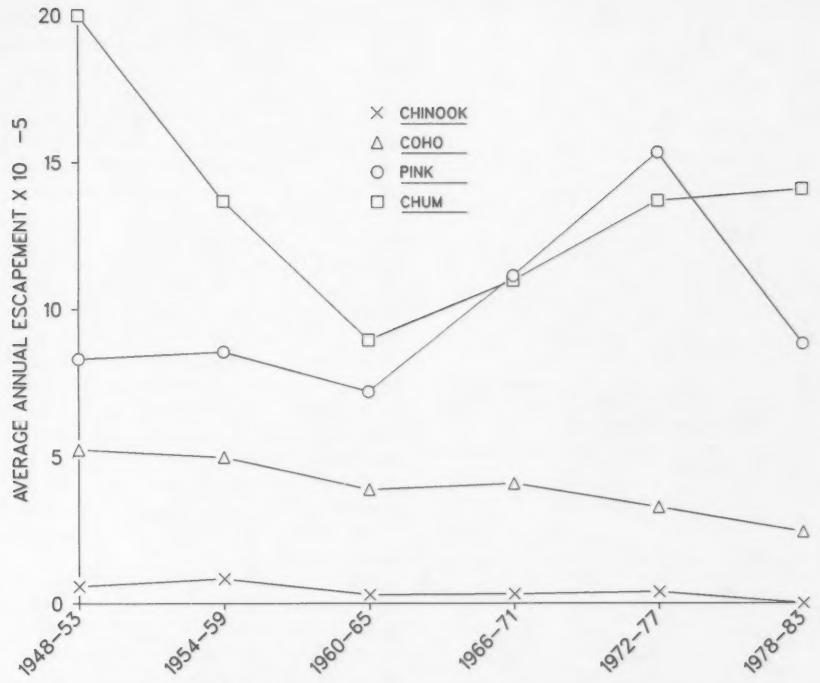

FIG. 2. Escapements of four salmon species to British Columbia statistical areas 11–27, averaged by 6-yr periods. The contribution of each stream to each period average was estimated from only those years in the period for which the stream had a recorded estimate (this convention corrects for decreases in reported escapement due to lack of field surveys in some years, especially 1980–82).

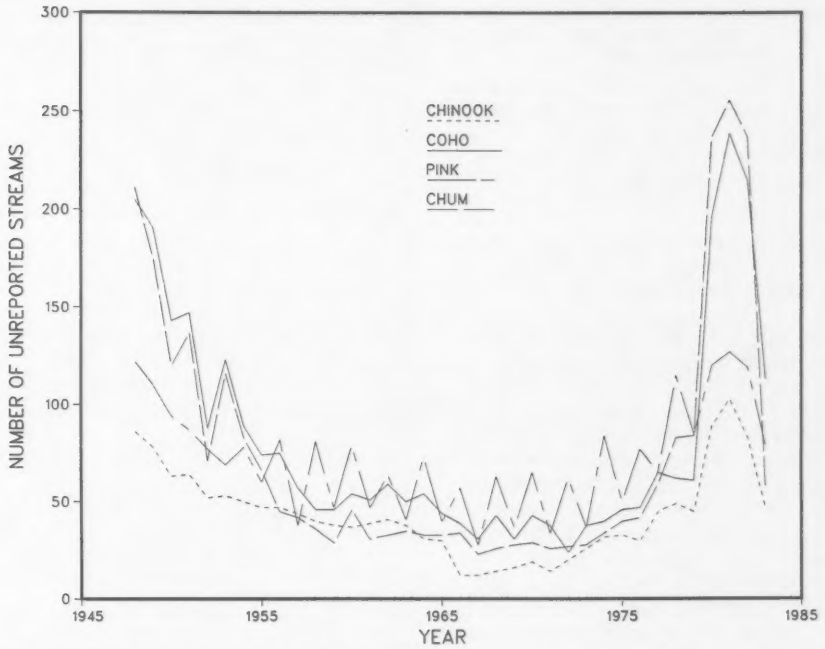

FIG. 3. Number of streams in British Columbia statistical areas 11–27 for which escapement estimates were reported by field staff as "not recorded" or "not available." For recent years these reporting codes were mainly used to indicate that no field survey had been made.

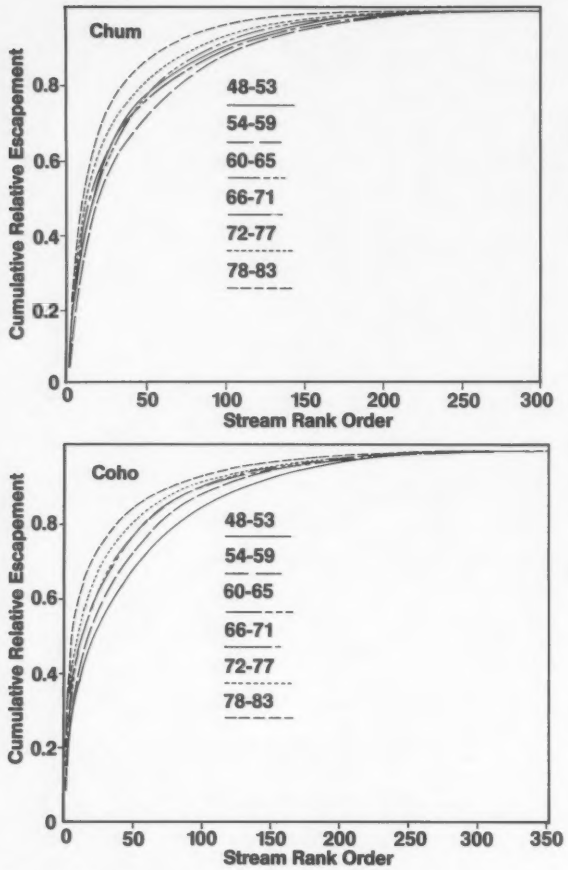

FIG. 4. Cumulative relative escapement as a function of stream rank order as in Fig. 1, except that the average escapement for each stream in each period is estimated from only those years in the period for which the stream had a recorded estimate. Compare with Fig. 1, where nonsurveyed stream – year cases were assigned an observed escapement of zero.

ity rates, (3) selective increase in a few stocks due to salmonid enhancement activities, and (4) changes in counting effort and methods. The last of these factors cannot be ignored, as noted above for coho.

Figure 3 shows time series of the number of streams in areas 11–27 for which escapement estimates were reported as "unavailable" (usually meaning no visit by field staff), "unknown," or "not recorded." For coho and chum, the majority of streams fell in these categories for 1980–82, and field staff have argued that this is due to loss of funding for seasonal field staff. However, this sampling problem does not fully explain the patterns shown in Fig. 1; a trend toward decreasing diversity is evident even when the average escapements for each time period are calculated using only the number of years (usually three rather than six for the 1978–83 period) for which estimates were actually recorded on each stream (Fig. 4). Comparing Fig. 1 and 4, it appears that roughly half of the decrease in apparent diversity for coho in the 1978–83 period can be explained by the sampling rate change for 1980–82.

Fishery officers have reported increased difficulty seeing fish in many streams, due to turbidity and flooding that they associate with logging and other habitat disturbances. However, such comments are temporally scattered throughout the records, and the most common disturbances involve mainly transient effects (lasting a few years) on turbidity and flow. Thus, the physical conditions for counting have probably not become cumulatively worse since 1950. Likewise, the records do not show a clear pattern of irreversible stock loss following reports of transient disturbance. There have been very few irreversible losses attributable to permanent habitat changes such as construction of hydroelectric dams.

Even if the changes shown in Fig. 1 can be attributed largely to decreases in counting effort rather than changes in real abundance, there is still considerable cause for alarm. Deterioration in the escapement monitoring system will eventually leave the Department of Fisheries and Oceans without an adequate data base to assess stock trends and impacts of regulatory measures. Also, habitat protection measures are now justified largely by arguments about loss in potential production rather than current, realized performance; such arguments may be challenged by other watershed users in the future, with demands that fisheries interests demonstrate the actual economic value of fish produced. Such demonstrations will require data on historical escapement levels.

Decreases in diversity have not been consistently associated with decreases in total escapement (Fig. 2). For pinks and chums, there have been deliberate efforts to rebuild escapements following a period of heavy exploitation in the 1950's (D. Anderson, DFO, Nanaimo, B.C., pers. comm.); it appears that these efforts have led to the selective recovery of a few more productive stocks, while the majority of (small) stocks have failed to respond. This failure may reflect the pressure of depensatory mortality agents that have caused reduced stocks to keep declining even after exploitation rates have been reduced. For chinook and coho, exploitation rates have been increasing at least since 1970 (Argue et al. 1983), and most escapements have declined accordingly; the main exceptions are systems subject to major salmon enhancement projects.

It should be noted that decreased stock diversity does not imply decreased total production in mixed fisheries. When the stocks cannot each be managed seperately, Paulik et al. (1967), Ricker (1973), and Hilborn (1985) have noted that the loss of some less productive units is practically inevitable. However, the price of this loss may include increased variability of catches, and increased vulnerability of the mixed fishery to disturbances of the remaining stocks. Beyond such statistical effects and risks, decreased diversity will mean lost opportunities for improved management in the future through measures such as terminal fisheries (where each stock can be harvested at a rate appropriate to its productivity) and culture of stocks with unique and desirable genetic characteristics.

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APPENDIX. The top 10 streams contributing to escapements for the species–time combinations plotted in Fig. 1. Asterisks in the 1978–83 column indicate streams where escapements may have been substantially influenced by salmonid enhancement projects (from Anonymous 1982).

	1948–53	1954–59	1960–65	1966–71	1972–77	1978–83
Chinook	Nimpkish	Cowichan	Klinaklini	Somass	Somass	Somass*
	Somass	Klinaklini	Somass	Cowichan	Cowichan	Cowichan
	Southgate	Nimpkish	Nimpkish	Toba	Campbell	Qualicum*
	Cowichan	Somass	Homathko	Campbell	Nimpkish	Southgate
	Nahmint	Puntledge	Southgate	Klinaklini	Toba	Homathko
	Klinaklini	Homathko	Cowichan	Nimpkish	Klinaklini	Marble
	Puntledge	Southgate	Campbell	Homathko	Southgate	Campbell*
	Homathko	Kingcome	Kingcome	Southgate	Homathko	Nanaimo
	Marble	Marble	Toba	Klite	Toba	Gold
	Tahsish	Nanaimo	Puntledge	Toba	Wakeman	Klinaklini
Coho	Somass	Cowichan	Cowichan	Somass	Somass	Qualicum*
	Cowichan	Somass	Somass	Cowichan	Cowichan	Cowichan
	Kakweiken	Kingcome	San Juan	San Juan	Qualicum	Somass*
	Nimpkish	Toba	Nimpkish	Nimpkish	Toba	Quinsam*
	Kokish	Nimpkish	Kingcome	Kingcome	Kingcome	Kakweiken
	Anuhati	Oyster	Koksilah	Toba	San Juan	Puntledge*
	Kingcome	Wakeman	Toba	Black	Demamiel	Marble
	Oyster	Toquart	Tsolum	Marble	Black	Homathko
	Quatse	Keogh	Oyster	Oyster	Koksilah	Toba
	San Josef	Anuhati	Black	Tsolum	Kakweiken	Black
Pink	Keogh	Skwawka	Glendale	Glendale	Kakweiken	Kakweiken
	Kakweiken	Glendale	Skwawka	Burman	Wakeman	Glendale
	Tsolum	Tsolum	Amor de Cosmos	Keogh	Glendale	Wortley
	Quatse	Kakweiken	Adams	Quatse	Kingcome	Wakeman
	Oyster	Keogh	Keogh	Grassy	Phillips	Anuhati
	Amor de Cosmos	Oyster	Phillips	Kakweiken	Burman	Grassy
	Skwawka	Toba	Burman	Amor de Cosmos	Adams	Phillips
	Adams	Adams	Toba	Nahwitti	Amor de Cosmos	Keogh
	Toba	Amor de Cosmos	Anuhati	Phillips	Grassy	Cluxewe
	Deserted	Deserted	Wakeman	Stranby	Keogh	Ahta
Chum	Cowichan	Viner	Qualicum	Qualicum	Qualicum	Southgate
	Nimpkish	Cowichan	Cowichan	Cowichan	Nitinat	Cowichan
	Qualicum	Nimpkish	Puntledge	L Qualicum	Orford	Qualicum*
	Chemainus	Nanaimo	L Qualicum	Sarita	Cowichan	Orford
	L Qualicum	Nahmint	Viner Sound	Nahmint	Sarita	Puntledge*
	Nanaimo	L Qualicum	Toba	Nitinat	L Qualicum	L Qualicum*
	Klinaklini	Sarita	Nitinat	Nanaimo	Puntledge	Sarita
	Nahmint	Puntledge	Nimpkish	Puntledge	Viner	Nanaimo*
	Puntledge	Qualicum	Tzoonie	Sooke	Nanaimo	Chemainus*
	Kakweiken	Toquart	Glendale	Viner	Sooke	Nahmint

PERSPECTIVES

Questions and Comments on the River Continuum Concept

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The River Continuum Concept (RCC) is a generalized conceptual framework for characterization of pristine running water ecosystems. Of the numerous tenets of the concept we particularly reevaluated the following: biological analogues of energy equilibrium and entropy in the physical system; maximization of energy consumption through continuous species replacement over a year; absence of succession in stream ecosystems, which can thus be viewed in a time-independent fashion; and maximization of biotic diversity in midreaches of streams as a result of the occurrence of highest environmental variability there together with spatial abundance shifts of insects, molluscs, and crustaceans. When emphasis is placed on rapid changes in the downstream hydraulics dependent on discharge and slope (both of which are expressed by stream order in the RCC and are key factors of the concept) and on results from tropical studies, some of these tenets are partly refuted or need extension. Some of them are in conflict with the current state of knowledge in other domains of stream ecology or are at least open to various interpretations. Therefore, we advocate modifications of the theoretical background of the RCC.

Le concept de continuum du milieu fluvial (CCMF) est un cadre conceptuel généralisé pour la caractérisation des écosystèmes lotiques vierges. Parmi les nombreux principes de ce concept, les auteurs ont réévalué en particulier les suivants : les analogues biologiques de l'équilibre énergétique et de l'entropie dans le système physique; la maximalisation de la consommation d'énergie par le remplacement continu des espèces au cours d'une année; l'absence de succession dans les écosystèmes lotiques qui peuvent donc être considérés indépendamment du temps; et la maximalisation de la diversité de la faune et de la flore dans les sections mitoyennes de cours d'eau, maximalisation due à la présence d'une variabilité environnementale optimale en plus de variations spatiales de l'abondance d'insectes, de mollusques et de crustacés. Certains de ces principes sont en partie réfutés ou doivent être élargis quand on met l'accent sur les variations rapides de l'hydrodynamique des eaux d'aval qui dépend du débit et de la pente (ces deux facteurs-clés du CCMF sont exprimés selon la position du cours d'eau dans le concept), et sur les résultats d'études du milieu tropical. Quelques-uns de ces concepts entrent en conflit avec les connaissances actuelles sur d'autres aspects de l'écologie lotique ou au moins peuvent être interprétés de diverses façons. Les auteurs recommandant donc des modifications des éléments théoriques du CCMF.

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The question of how headwater and downstream ecosystems vary in structure and/or function was and remains a central issue of running water ecology. At the beginning of the 1970's a group of North American stream ecologists started a new approach to this question, which resulted in the River Continuum Concept (RCC) (Vannote et al. 1980). The authors of the concept consider it as a framework for a characterization of pristine running water ecosystems, "describing the structure and function of communities along a river system" in relationship to the abiotic environment. The RCC stimulated immediate comment and avid discussion (Winterbourn et al. 1981; Barmuta and Lake 1982; Culp and Davies 1982; Hauer and Stanford 1982; Taylor and Roff 1982; Winterbourn 1982; Cole 1983; Gray et al. 1983; Rounick and Winterbourn 1983; Stanford and Ward 1983; Ward and Stanford 1983; Townsend and Hildrew 1984[1]). Recent contributions from the RCC proponents (Cummins et al. 1983; Cushing et al. 1983; Minshall et al. 1983; Bruns et al. 1984) modify some ideas of Vannote et al. (1980), but generally support the RCC. From personal discussions and unpublished manuscripts we gather that further modifications and clarifications of the RCC

[1]Paper delivered at the SIL meeting in Lyon 1983. Here and in other cases we refer to the oral presentation and the abstract.

can be expected from its proponents (e.g. Sedell and Froggatt 1984; Cummins et al. 1984).[2]

During an analysis of the information available on the RCC we realized that some of its basic assumptions or tenets, as we interpret them, affect the domain of stream ecology to a greater degree than is evident at first glance and certainly more than is discussed in the above papers. Some tenets are at variance with our view of the current state of knowledge. Other assumptions can be interpreted in various ways and require clarification.

We will discuss some of these assumptions briefly, concentrating particularly on five tenets: biological analogues for (1) energy equilibrium and (2) entropy pattern in the physical system; (3) maximization of energy consumption through continuous species replacement over a year; (4) absence of succession in stream ecosystems, which can thus be viewed in a time-independent fashion; and (5) maximization of species diversity in midreaches of streams as a result of the occurrence of the highest environmental variability there and spatial abundance shifts of insects, molluscs, and crustaceans.

The aim of this paper is to suggest some modifications in the theoretical background of the RCC. But first we would like to stress that we accept many parts of the RCC as they stand and respect the scientific ideas that our North American colleagues have compiled in their framework.

General Remarks on the RCC

Before we deal with the five RCC tenets mentioned above, some of the general aspects of the concept as well as the limitations contained in it will be briefly outlined and commented on.

The main goal of the RCC is to link fluvial geomorphic processes, physical structure, and the hydrologic cycle to "patterns of community structure and function and organic matter loading, transport, utilization and storage along the length of a river." This is very expressively illustrated in Vannote et al. (1980, Fig. 1), in which the influence of riparian vegetation, the status of trophy, load, transport, and the relative importance of functional feeding groups (shredders, collectors, etc.) is related to stream order (Leopold et al. 1964) as an expression of the physical component. However, as stream order is not, in any case, a meaningful description of the physical environment (Gregory and Walling 1973), it should be regarded only as an indication of the relative position of a stream reach within the entire running water system. A physical characterization of each reach under study must therefore be added.

The RCC as published in 1980 includes qualifications about certain environmental situations. Some of the criticisms of the RCC so far published are not appropriate when these limitations and modifications (Vannote et al. 1980) to the RCC are taken into account: (i) the RCC has been developed for natural, unperturbed stream ecosystems; (ii) streams at high elevations and latitudes, xeric regions, and deeply incised valleys may deviate from the general pattern with regard to autotrophy/heterotrophy; (iii) tributaries entering the main stream have localized effects of varying magnitude depending on the volume and the nature of the input.

The RCC does not particularly deal with the various types of sources (limnocrene, helocrene, rheocrene) and mouths (delta, estuary) of stream systems (see Fig. 3) nor does it mention natural lakes that occupy intermediate positions on the "river continuum." And, a fact we regard as very important, the RCC is not restricted to a certain geographical area, i.e. we consider it a concept of worldwide applicability.

Classification of the benthic invertebrates into functional feeding groups (Cummins 1974) is a fundamental attribute of the RCC, and stresses the importance of ecological functions. We applaud this approach, which, however, poses some practical problems: the diet of a macroinvertebrate species can be varied, depending on age (e.g. Schröder 1976; Fuller and Stewart 1977) as well as on site (e.g. Martinson and Ward 1982; Williams and Williams 1982).

Special problems are posed when ecological study involves assumptions about unperturbed stream conditions, because our knowledge of the ecology of pristine headwater streams is scarce and of pristine rivers is almost nonexistent (see Horwitz 1978; Sedell and Luchessa 1982). Hence, such an approach is necessarily based to some extent on speculation. We explicitly welcome the RCC's endeavour to describe natural stream ecosystems, since in most cases this may be the most appropriate way to illustrate the deviations of our "modern" streams from their historic nature.

Today, most lower reaches of streams have been radically changed by human activities. The original condition of certain stream systems in North America have been demonstrated in a fascinating way by Sedell and Froggatt (1984) and Triska (1984): riparian trees from eroded banks formed large organic debris dams, blocking the channel, creating lakes, new side channels, and so on. A similar situation occurred in Europe. Behning (1928) described a unique biocoenosis on trees washed into the Volga. And there is historical evidence that in the twelfth century, servants on horseback had to guide ships through the Oder in order to avoid collisions with the dangerous oak trees lying in the river (Herrmann 1930). Besides the main channel, smaller ones occurred with flow characteristics resembling those in reaches further upstream (Krause 1976). Similar conditions have been described in the Amazon (Junk 1982; Sioli 1982) and the Congo (Stanley 1874–77). This "original state" of larger pristine rivers was not considered in Vannote et al. (1980): thus, we will discuss its consequences for the RCC below.

On Five RCC Tenets

Tenet I: Energy Equilibrium of the Physical System and Biological Analogue

In our opinion the central statement of the RCC is that "biological communities should become established which approach equilibrium with the dynamic physical conditions of the channel" (Vannote et al. 1980, p. 132). To understand this statement we must go back to Leopold et al. (1964, p. 266 ff) who discussed in detail the physical dynamic equilibrium of streams: power expended per unit length of a channel and per unit area of the bed of a channel (Table 1) are expected to tend to uniformity. A modal value of central tendency between the two will lead to a longitudinal equilibrium profile of the channel.

Recently, Mangelsdorf and Scheurmann (1980) took a physical–analytical approach to the question of the equilibrium profile, giving examples and discussing the situation in streams that have almost reached or are far from their equilibrium profile. They stress that tectonics, lithology, and climate determine the longitudinal profile of each running water in a characteristic way. Thus, for example, the Rhine has three base

[2]See also Minshall et al. in this issue (Ed.).

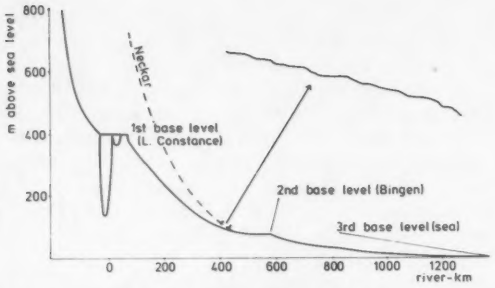

FIG. 1. Rough slope curve of the Rhine and the Neckar (according to Mangelsdorf and Scheurmann 1980). The Rhine has three base levels: lake level of Lake Constance (its depth is indicated by the two loops), slate formation at Bingen, and sea level at the mouth (indicated by the thin straight line). The arrow points to a detail in the slope curve of the Neckar above Heidelberg (according to Wilser 1937).

levels (Fig. 1): Lake Constance, Bingen (due to slate), and, finally, the sea, i.e. at present the Rhine is approaching an equilibrium profile in three sections. This is due to the very "turbulent" history of the Rhine, into which other basins were incorporated (Quitzow 1976–77). The Neckar is included in Fig. 1. If we take a closer look at its profile above Heidelberg, in an area with a high tectonic diversity, the influence of location-specific events on a stream profile can be demonstrated. These two examples show that empirical–statistical models of the physical state of a stream system cannot be used without checking if the models are valid for these streams.

System-characteristic runoff patterns, which are assumed to modify the progressive and predictable change in the physical system (Minshall et al. 1983), will further complicate the RCC. In Europe, 60 different types of runoff patterns are characterized (Grimm 1968), which can be altered on the microscale by basin shape and relief (Gregory and Walling 1973, fig. 5.10).

In principle, however, it can be stated (Mangeldorf and Scheurmann 1980, p. 148) that a stream does tend towards that profile at which, for a given discharge, the material imported will be transported. If material input and transport capacity are not in equilibrium the stream starts to erode or to accumulate. Generally, a stream with a source in the mountains and no additional base level along its course to the mouth can then be divided into three sections: an upper reach, where erosion is dominant; a middle reach, which represents a zone of transition; and a lower reach, where accumulation prevails. Since the ratio of material input to transport capacity is not constant at a given point of the stream over time — in addition to more regular annual variations, irregular episodic changes occur (Bergstrom 1982; Kelsey 1982) — the limits between these three reaches shift upstream and downstream according to discharge and material load. Hence, the reach with the highest dynamics is the middle one where the slope levels off. In this area natural streams are frequently braided at first and then start to meander. Where a stream is braided, there is a frequent decrease or increase in channel number and a variety of channel characteristics, depending on the discharge (Mosley 1982).

We are not sure whether biological consequences of the dynamic equilibrium of a stream discussed by Curry (1972, p. 13), in a paper cited in the RCC under the heading "Derivation of the concept," are implicitly included in the RCC or not. Curry considered that the energy of the physical system, which is expended as frictional heat energy, is "of great importance as energy input in biologic communities." Therefore the tendency toward uniformity of energy expenditure in river systems will help to explain the stability and diversity of stream communities. Are these ideas covered by the following RCC statement: "The tendency of the (physical) river to maximize the efficiency of energy utilization and the opposing tendency toward a uniform rate of energy use" (Vannote et al. 1980, p. 131), which is another way to express the dynamic equilibrium condition of a channel, has an analogue in the trade-off of the biological system between the tendency "to make most efficient use of energy inputs" (e.g. through resource partitioning of *temperature*) and the tendency "towards a uniform rate of energy processing throughout the year" (Vannote et al. 1980, p. 134)? And what is the meaning of "a tendency for reduced fluctuations in energy flow" of "river ecosystems" (p. 133) or a tendency of "stream ecosystems ... towards uniformity of energy flow on an annual basis" (p. 134) (Vannote et al. 1980)? Does this imply an energetic unity of the physical and biological system? If so, the annual variations in physical energy flow (e.g. discharge) must be counterbalanced by the biological energy flow in order to reach uniformity on the ecosystem level (= abiotic + biotic energy flow tend to uniformity).

Since these energy statements have a great impact on the theoretical background of stream ecology, they require clarification by its authors.

From the above it is evident that the energy expenditure of the physical system plays an important role in the RCC. However, recent contributions on the RCC have not concentrated on hydraulics. For example, only a short sentence in Minshall et al. (1983, p. 18) was devoted to this subject. Thus, we used the data from the 16 stations investigated in that study to calculate some simple physical parameters such as power expended per unit of length and area, shear stress, and Froude number, which gives an indication of turbulence in streams (streaming or shooting flow; see Table 1 for formulae). No modal value of central tendency between power/reach and power/area is indicated by the downstream pattern of these parameters (Fig. 2). Neither do Froude number and shear stress exhibit uniform tendencies (Fig. 2). The causes of this may be that (i) available discharge data are annual means and not bankfull discharges, (ii) the streams studied were not within the limits set by the dynamic equilibrium theory of streams, (iii) in three of the four study sites the lowermost stations did not receive water from the upper stations, and (iv) the location-specific lithology and geomorphology modified the general tendency expected at several stations; such a tendency is, of course, difficult to discern at only four stations over stream reaches 35–57 km long.

To demonstrate the relationship between stream geomorphology (e.g. slope), the physical properties of flow near the stream bottom, and aquatic invertebrate ecology, we will introduce another parameter here: the thickness of the laminar sublayer above the stream bottom. Distribution patterns of benthic invertebrates are related to this indicator of the actual forces acting at the stream bottom, i.e. "hydraulic stress" (Statzner 1981a, 1981b). This sublayer equation (formula 5 in Table 1) incorporates, in principle, the same parameters as the Manning formula (6 in Table 1), which can be transformed into the sublayer equation and vice versa (Smith 1975). If the Manning formula is written differently (6′) and compared with formula 5, it becomes evident that the thickness of the laminar sublayer is

TABLE 1. Formulae used for the expression of physical patterns along the course of streams (note that the Manning formula (6) is written for wide channels with a simplified roughness parameter).

(1) $P_1 = QgS\rho$ (2) $P_2 = \frac{QgS\rho}{w}$

(3) $\tau_0 = gDS\rho$ (4) $\mathrm{Fr} = \frac{U}{\sqrt{gD}}$

(5) $\delta' = \frac{11.5\nu \; 5.75 \log\left(\frac{12D}{r_p}\right)}{U}$

(6) $U = \frac{\text{const.}}{r_p} D^{2/3} S^{1/2}$ (6′) $\frac{1}{S} = \left(\frac{\text{const.} \; D^{2/3}}{\frac{r_p}{U}}\right)^2$

NOTE: D = channel depth (m), Fr = Froude number, g = acceleration due to gravity (m/s^2), P_1 = power per unit length of a channel (W/m), P_2 = power per unit area of a channel (W/m^2), Q = discharge (m^3/s), r_p = roughness of channel bottom (m), S = slope (m/m), U = mean current velocity (m/s), w = channel width (m), δ' = thickness of laminar sublayer (m), ν = kinematic viscosity (m^2/s), ρ = density of water (kg/m^3), τ_0 = shear stress (N/m^2).

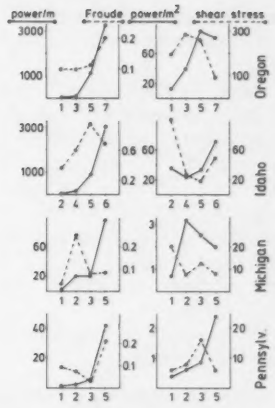

FIG. 2. Parameters for energy expenditure (see Table 1 for formulae and units) at the 16 RCC stations considered by Minshall et al. (1983). Note that no uniform patterns emerge on the way downstream (x-axes: stream orders), if the complete set of data is considered.

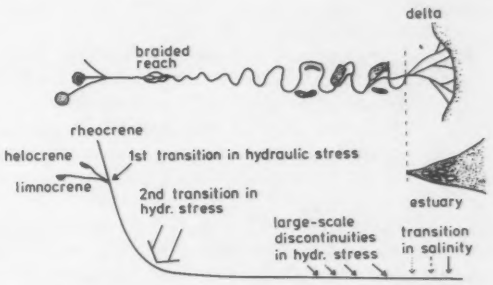

FIG. 3. Some typical changes in the central tendency of habitat characteristics from the source to the mouth in a hypothetical pristine stream. Not all of the components shown here can be or must be present in a stream system.

also related to slope (Statzner 1981a): an increase in slope should reduce the thickness of the laminar sublayer, hence raising the hydraulic stress on the stream bottom and vice versa. We have thereby linked a central tendency of microhabitat characteristics in a reach ("hydraulic stress") to a macrohabitat characteristic ("slope"): the latter "are major determinants of the types of microhabitats," to which fish as well as invertebrates respond (Bovee 1982, p. 3). It should be noted here that these formulae (5, 6, 6′) as written in Table 1 are not applicable to all hydraulic situations found in natural streams (Bovee and Milhous 1978; Statzner 1981a), and they are used here as vehicles to elucidate some of the physical patterns one can expect along a stream course.

Summing up the above, we suggest the following characterization of an "ideal" or "standard" pristine running water course (Fig. 3) to which real streams can be compared. The source and the first part of its effluent are frequently characterized by relatively low hydraulic stress. A transition zone is followed by a reach of high hydraulic stress, which, after the next zone of transition at the break-point of the slope curve (we regard the values of bed slope, hydraulic slope, and energy slope as identical), is then followed by a zone of lower hydraulic stress. Further downstream, numerous large-scale discontinuities of the hydraulic stress occur. How the mouth of a stream system entering the sea is developed depends mainly on the material exported by the stream and the transport capacity of the marine component, including tidal amplitude and other currents (Mangelsdorf and Scheurmann 1980). The role of the stream in this context has been illustrated in "large-scale experiments": reduction of material transported by the stream due to artificial dams reduces the area of the original delta (Baxter 1977). The main types of mouths are estuaries and deltas (Fig. 3), and it is important to note that the physical characteristics of the stream influence in part the salinity at the mouth of the stream.

We conclude that the pattern of physical parameters as proposed in Fig. 3 obviously does not represent a "continuous" or "intergrading" gradient as dictated by the RCC (Vannote et al. 1980; Cushing et al. 1983), and variations on the microscale as well as lakes and other additional base levels will complicate matters much more. Thus, the analogies between the physical and the biological equilibrium of streams cannot be as simple as suggested by the RCC.

Tenet II: Entropy Patterns

In addition to energy statements discussed above, some clarification is required about a statement on entropy: from headwaters to the mouth there is a constant gain in the physical variable "entropy." Vannote et al. (1980, p. 132) postulate that "the biological organization in rivers conforms structurally and functionally to kinetic energy dissipation patterns of the physical system."

Does this imply a characteristic tendency in biological entropy from the source to the mouth of a stream? The longitudinal organization of the gross photosynthesis/respiration ratio in the stream (thermodynamic concept of entropy) or the species diversity (e.g. Shannon index: entropy concept of information theory) can serve as indicative parameters. Both are considered in the RCC (Vannote et al. 1980, fig. 2), and in contrast with

the constant entropy gain in the physical system, both show increasing as well as decreasing tendencies on the way downstream.

Or does the entropy statement imply that the biological communities will adjust to the physical entropy pattern through energy consumption and processing, resulting in similar tendencies in the biological entropy in every reach of the stream? This is, of course, a usual tendency of organisms, since "living systems" are "negentropic" (Fränzle 1978).

We believe that the absence of this theoretical background will not mean a loss in significance of the RCC; thus, we suggest omitting the above statement on entropy.

Tenet III: Temporal Sequence of Species Replacement and Utilization of Energy Inputs

After a species has completed its growth "it is replaced by other species performing essentially the same function ... It is this continuous species replacement that functions to distribute the utilization of energy inputs over time" and results in a composite species assemblage tending to "maximize" energy consumption (Vannote et al. 1980, p. 134). This tenet may be applicable only to stream systems in geographical zones subject to distinct seasonal variations in abiotic factors.

A temporal sequence of species replacements, such as postulated by the RCC based on experience from North America, has already been rejected by Winterbourn et al. (1981) and Towns (1983) for streams in New Zealand. In equatorial regimes, all principal species of a stream system are present over the whole year. This is clearly demonstrated by emergence data of four insect groups from a stream situated 2°S in Zaire (Zwick 1976; Statzner 1976; Lehmann 1979; Kopelke 1981): no complete temporal replacement occurs, although several species show cyclic patterns. The terrestrial vegetation in this latitude does not exhibit a distinct phenology comparable with that of temperate zones, but periodic patterns obviously do occur (Dieterlen 1978). This suggests some seasonality in the input of course organic material into the stream communities, which is probably processed faster in the tropics than in temperate climates (Dudgeon 1982). The question is whether such stream communities near the equator have developed other possibilities to "maximize" energy consumption. Fittkau (1973) suggests that the high efficiency of energy utilization is linked to a high species number and a relatively low abundance of each species in Central Amazon streams which are scarce in nutrients.

Another question is whether the species assemblage of a stream reach really plays the role postulated by the RCC. Minimization of leakage (export of organic compounds) from a stream reach is another way to express maximization of energy consumption. Recent studies have shown that leakage is reduced under normal discharge conditions if the invertebrate fauna is destroyed in experiments or in computer simulations (Wallace et al. 1982; Webster 1983; see also Meyer and O'Hop 1983), i.e. macroinvertebrates decrease the efficiency of stream ecosystems.

Tenet IV: Time Invariance and Absence of Succession in Stream Ecosystems

Vannote et al. (1980, p. 135) stated that the temporal change of the biological system of a stream "becomes the slow process of evolutionary drift" and the community "gains and loses species in response to low probability cataclysmic events and in response to slow processes of channel development." As a result of this, succession in stream ecosystems is absent and these systems can be viewed in a time-independent fashion.

If we accept cataclysmic events as a factor that causes gains and losses of species, then we might expect that the biological community in the stream is reestablished afterwards by means of succession (see Fisher 1983) parallel to that in the terrestrial environment (e.g. after landslides, wildfires, or volcanism).

In our opinion, succession cannot, therefore, be rejected in stream communities. As a consequence, stream ecosystems cannot always be viewed in a time-independent fashion. And we have evidence from long-term studies that time invariance does not occur: this is demonstrated for insects (Illies 1978, 1982) and fish (Grossman et al. 1982). While discussing organic matter budgets for stream ecosystems, some authors of the RCC drew a similar conclusion in a recent paper (Cummins et al. 1983).

Tenet V: Pattern of Biological Diversity

This tenet of the RCC, discussed at some length, states that high environmental variation results in high biotic diversity. This concept was actually first formulated early in this century by Thienemann in one of his biocoenotic principles (see Hynes 1972, p. 234).

In Vannote et al. (1980) the variation of the environment is discussed using the example of the diel water temperature amplitude, which is certainly highest in the midreach of a natural stream in temperate climates. The RCC indicates that the biological diversity is therefore also highest in the midreach (Fig. 4D). However, if we include the annual amplitude of the water temperature (i.e. as a second environmental factor), the highest variability no longer occurs in the midreach of our stream. And it is very improbable that all other factors mentioned by the RCC, such as riparian influence, substrate, flow, and food, show their highest variability exactly in the midreaches of streams (see also the conclusion at the end of tenet I). The latter holds especially true if we include non-temperate climates. Tropical streams may have very low diel and annual temperature amplitudes in their middle and even lower reaches (e.g. Sioli 1975; Statzner 1975).

A second explanation of the RCC for the maximum of species diversity in the midreach of streams is the convergence of two vectors that illustrate shifts in spatial distribution (Vannote et al. 1980, p. 135): insects are believed to have become aquatic first in headwater streams, while molluscs and crustaceans have reached streams from the marine environment through the mouth of streams. Later, insect abundance shifted downstream and mollusc and crustacean abundance shifted upstream.

The confluence of these migratory vectors might cause high diversity (e.g. Shannon index) in the midreach only if insects shifted at the same speed downstream as molluscs and crustaceans shifted upstream, but not during the phase of complete overlap of the abundance patterns (Fig. 4A–4C). We see no evidence to suggest that these conditions are fulfilled in nature, especially not in most streams. On the other hand, existing evidence shows that, excluding effects of pollution, diversity in streams may change drastically bearing no relation to the "order" of that stream (Statzner 1981c) or that diversity is almost constant throughout different "orders" (Minshall et al. 1982).

A large part of the discussion of this topic dealt with benthic macroinvertebrates, which, of course, contribute only part of the complete community diversity. It is, for example, a well-known fact (and also shown by Vannote et al. 1980, fig. 1)

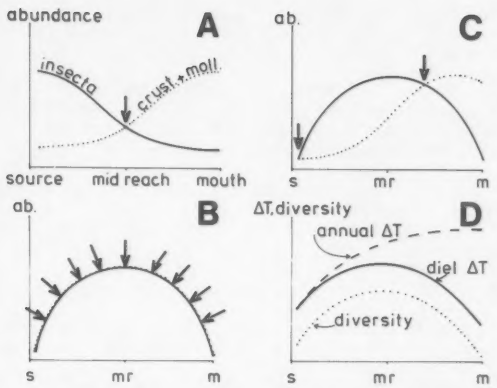

FIG. 4. (A–C) Hypothetical abundance distribution of Insecta, Crustacea, and Mollusca shifting downstream or upstream, respectively, and the consequences for a diversity index (e.g. Shannon), which is highest (arrow) where the abundance of all species is the same. (A) Beginning of shift, both groups shifting with the same speed; (B) complete overlap, both groups shifting with the same speed; (C) Insecta shifting faster downstream than Crustacea and Mollusca upstream. (D) Development of the diel and annual water temperature amplitude and the diversity, as suggested by the RCC, from the source to the mouth of a stream. See text for discussion of these patterns.

that plankton develops mainly in the lower reaches of streams, and the number of fish species increases there also. This will, of course, influence the diversity pattern of the complete community, which is probably at its highest in the lower reaches of streams, where the large-scale discontinuities in hydraulic stress occur (Fig. 3). Furthermore, the environmental variability of a particular physical structure may influence the diversity of one group (e.g. insects) in a different way than that of other groups (e.g. fish) (Schlosser 1982).

Conclusion

The five tenets of the RCC discussed above are open to various interpretations, need extension, or are unexpected or refuted by the current state of knowledge. The physical parameters in streams obviously do not exhibit a continuous or intergrading gradient (tenet I) in the downstream direction (Fig. 3). Thus, biological analogues of the energy equilibrium in the physical system are more complicated than suggested by the RCC. It is not clear how the RCC relates entropy patterns of the biological to the physical system (tenet II). Since we do not see an essential need for the statement on entropy in the RCC, we recommend its omission from the concept. This will reduce the theoretical ballast of the RCC. Maximization of yearly energy utilization through species replacement (tenet III), lack of succession and time invariance in stream communities (tenet IV), and specific mechanisms leading to high biotic diversity in midreaches of streams (tenet V) are either rejected (IV), unexpected (V), or restricted to particular geographical areas (III). We therefore suggest modifying the original RCC by excluding tenets III–V from the concept. This will result in a higher flexibility and larger applicability of the RCC.

In our opinion, these modifications will hardly conflict with projects relating to the RCC that have been realized up till now (see Minshall et al. 1983 and references therein; Cummins et al. 1983; Cushing et al. 1983; Bruns et al. 1984). These projects placed emphasis on gross photosynthesis and respiration and on the status of organic matter and the corresponding functional organization of the community, i.e. on points that we evaluate as major objectives of the RCC. None of these is directly restricted by the recommended modifications.

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Developments in Stream Ecosystem Theory[1]

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Four significant areas of thought, (1) the holistic approach, (2) the linkage between streams and their terrestrial setting, (3) material cycling in open systems, and (4) biotic interactions and integration of community ecology principles, have provided a basis for the further development of stream ecosystem theory. The River Continuum Concept (RCC) represents a synthesis of these ideas. Suggestions are made for clarifying, expanding, and refining the RCC to encompass broader spatial and temporal scales. Factors important in this regard include climate and geology, tributaries, location-specific lithology and geomorphology, and long-term changes imposed by man. It appears that most riverine ecosystems can be accommodated within this expanded conceptual framework and that the RCC continues to represent a useful paradigm for understanding and comparing the ecology of streams and rivers.

Quatre importantes lignes de pensée fournissent une base pour l'élaboration d'une théorie détaillée sur les écosystèmes lotiques : (1) l'approche holistique; (2) le lien entre les cours d'eau et leur emplacement terrestre; (3) le cycle de matières dans les systèmes ouverts; et (4) les interactions biotiques et l'intégration des principes sur l'écologie des communautés lotiques. Le concept de continuum du milieu fluvial représente une synthèse de ces idées. On présente des suggestions pour l'éclaircissement, l'expansion et le perfectionnement de ce concept de façon à y inclure des échelles spatiale et temporelle plus larges. Sous ce rapport, les facteurs importants comprennent le climat, la géologie, les tributaires, la lithologie et la géomorphologie de chaque emplacement et les perturbations humaines à long terme. Il semble que la plupart des écosystèmes fluviaux peuvent être inclus dans cette structure conceptuelle élargie et que le concept de continuum représente toujours un paradigme utile pour comprendre et comparer l'écologie des ruisseaux et des rivières.

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At the beginning of this century, limnologists studying streams focused in great detail on the morphology, life cycles, behavior, and trophic relations of stream organisms (e.g. Steinmann 1907; Wesenberg-Lund 1911; Thienemann 1912). The observed diversity of the stream biota led several researchers to seek simplifying generalities in terms of the observed fauna (e.g. Steinmann 1915; Thienemann 1925; Carpenter 1928; Needham and Lloyd 1930). These early efforts stressed observation, and although a quantitative approach was soon adopted, the approach and the investigations conducted through the 1950's were largely descriptive and autecological in nature. Since that time, the direction of stream research has changed to incorporate a more synecological and holistic approach. In the following we briefly discuss four major areas in

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TABLE 1. Major areas in which developments in stream ecosystem theory have taken place in the past decade.

1. Progression from an individualistic to a holistic viewpoint
2. Realization of the critical linkage between a stream and its terrestrial setting
3. Development of ideas about material cycling in open systems
4. Recognition of the importance of biotic interactions to the stream community

which changes in perspective regarding stream ecosystems have occurred (Table 1) and which we believe form the foundation for further advances in stream ecology. With this foundation in mind, we then propose several adjustments to our earlier concept of riverine ecosystem dynamics (Vannote et al. 1980) which have grown out of our continued interest in this area (Cummins et al. 1983; Cushing et al. 1983b; Minshall et al. 1983, 1985; Petersen 1984; Sedell and Froggatt 1984; Vannote and Minshall 1982) and out of recent studies by others.

Major Contributions in Stream Ecosystem Theory

Progression from an Individualistic to a Holistic Viewpoint

A truly holistic view of streams as ecosystems did not begin until the late 1950's, being strongly influenced by Eugene and Howard Odum (e.g. Odum 1957; Teal 1957) and Ramon Margalef (e.g. Margalef 1960). The energy budget approach of Odum for stream segments led to a flood of stream ecosystem budgets (Warren et al. 1964; Mann et al. 1972; Hall 1972; Fisher and Likens 1973; Westlake et al. 1972) for both large and small streams which has continued to the present (Cummins et al. 1983).

The past 10 yr also have seen a shift in perspective from that of viewing streams, or different stretches within a stream, as individual entities to that of a synthetic (integrated) view which seeks generalizations about streams as ecosystems (e.g. Cummins 1974; Webster 1975; Wallace et al. 1977; Newbold et al. 1982a, 1982b; Minshall 1978; Minshall et al. 1983b). The prevalent synthetic view of stream ecosystems is that of the River Continuum Concept (RCC) (Vannote et al. 1980), its antecedants (see Ide 1935; Margalef 1960; Illies 1961; Hynes 1963; Ross 1963), and correlaries (Wallace et al. 1977; Newbold et al. 1981, 1982a, 1982b; Elwood et al. 1983; Ward and Stanford 1983) which emphasize the unifying aspects of flowing water (particularly geomorphology and fluid hydraulics) in structuring stream communities and providing a templet for stream ecosystem function. Historically, a number of stream ecologists have recognized shifts in community structure along the course of a river. Most focused on macroinvertebrates and fish (see papers reviewed by Hawkes 1975) and many viewed the relationship as a series of distinct zones (Illies 1961) rather than a gradually integrating continuum (but see Maitland 1966). Few attempted to treat streams and rivers holistically, and particularly to view them as ecological systems (e.g. Rzoska 1978). Margalef (1960) and Mann (1979) are noteworthy exceptions.

The RCC (Vannote et al. 1980) conceptualizes the entire fluvial system as a continuously integrating series of physical gradients and associated biotic adjustments. Streams are seen as longitudinally linked systems in which ecosystem-level processes in downstream areas are linked to those in upstream areas. This approach has provided useful generalizations concerning the magnitude and variation through time and space of the organic matter supply, the structure of the invertebrate community, and resource partitioning along the length of a river. These views are summarized by Cushing et al. (1983b) who stated, "... streams are best viewed as gradients, or continua, and that classification systems which separate discrete reaches are of little ecological value." The RCC is undergoing evolution, testing, and refinement — some aspects of which will be addressed below. However, even if nothing else were to come from it, this paradigm has served to focus attention on rivers as integrated systems and to stimulate the formulation and testing of systems-level hypotheses which have helped to move lotic ecology from a descriptive to a predictive mode.

Realization of the Critical Linkage between the Stream and Its Terrestrial Setting

Illies (1961), Illies and Botosaneanu (1963), and Ross (1963) were among the first to note similarities among stream communities over broad geographic areas. Ross in particular was struck by the association between stream macroinvertebrates and terrestrial biomes or what he termed the landscape aspect. He postulated the importance to the stream of the combination of climatic conditions necessary for the existence of such vegetation zones plus the factors imposed by the physical nature of the vegetation itself. The importance of the land–stream interaction also is implicit in the watershed approach to the study of terrestrial ecosystems (e.g. Likens et al. 1977).

Also in the early 1960's, Hynes (1963) published the first of a series of studies which drew attention to the importance of terrestrially derived (allochthonous) detritus to stream dynamics. He summarized the importance of the stream–land linkage in his paper "The stream and its valley" (Hynes 1975). Among other things, he noted that the slope of the valley, the depth and permeability of the soil, and the patterns of precipitation greatly affect the pattern of flow and dissolved organic matter content of the stream. Hynes (1975) and others have stressed the importance of the type and density of the terrestrial vegetation and of its chemical and biological dynamics once it reaches the stream. The pioneering work in this area emphasized conditions in streams draining forests and consequently, allochthonously derived organic matter. But the broader implication of these studies is clear: the terrestrial setting for the stream — be it forest, desert, taiga, or grassland — is crucial to the operation of stream ecosystem processes. Additional support for this idea has come from investigations by Fisher and Likens (1973), Minshall (1978), Cushing et al. (1980), Fisher et al. (1982), Molles (1982), Cummins et al. (1984), Minshall et al. (1983b), Naiman (1983), Strayer (1983), and others. Early research on the importance of allochthonous detritus has in turn given rise to additional major developments in the processing of this material, particularly by microbes (see reviews by Anderson and Sedell 1979 and Bird and Kaushik 1981).

Prior to a surge of interest in the role of allochthonous detritus in streams, considerable attention had been given to the primary producers (e.g. Butcher 1932, 1933, 1940, 1946; Blum 1957; Douglas 1958; Gumtow 1955) and to their role in stream food chains (e.g. Percival and Whitehead 1929; Jones 1950). With the interest generated by almost continuous breakthroughs in the area of allochthonous detritus dynamics, the important supportive or primary role of autotrophy in stream ecosystems was virtually ignored. By the mid-1970's, however, stream researchers began to direct their attention outside of forested

headwater streams. It became clear in the broader river basin and interbiome contexts, as well as in moderately shaded headwaters everywhere, that autotrophs contribute significantly to ecosystem dynamics in both the mass and quality of material they provide (Minshall 1978). Now it is generally recognized that both terrestrial plant debris and aquatic primary production are important sources of simple carbon compounds and that they commonly complement one another, both seasonally and along a river, to provide a more reliable and varied food base for lotic consumers than either would do alone (Hornick et al. 1981; Cushing and Wolf 1982; Gregory 1983).

Development of Ideas on Material Cycling in Open Systems

Webster (1975) pointed out that nutrients in a stream do not cycle in place, but are displaced downstream as they complete a cycle. He described this coupling of transport and cycling as "spiraling" and suggested that the ability of a stream to utilize nutrients is associated with the tightness and magnitude of the spirals. Webster (1975) and Webster and Patten (1979) proposed nutrient spiraling as a mechanism to account for the apparent ability of stream ecosystems to withstand and recover from disturbance. Later, Wallace et al. (1977) applied the idea in describing the role of filter feeders in streams. They suggested that filter feeders, through their capture of seston, impede the downstream transport of organic matter and serve to reduce the distance between spirals. The present state of our knowledge in this area is largely a result of the mathematical models developed by Newbold and his colleagues at Oak Ridge National Laboratories (Newbold et al. 1981, 1982a, 1982b; Elwood et al. 1983). These collective studies are termed the nutrient spiraling concept.

In four stream systems studied in an interbiome test of the RCC (Minshall et al. 1983b), all first-through third-order stations had "tight" spirals associated with a high retention capacity; the larger stream locations (fifth- to seventh-order) all had long distances between spirals. Rate of recycling was considered "fast" for about half of both the small- and large-sized streams, indicating differences in degree of biological influence (Minshall et al. 1983b). But in all streams studied, spiraling distance was determined primarily by current velocity and the presence and effectiveness of physical retention devices; biological processes played a lesser quantitative role. Thus, in many cases, the retentive capacity of the stream exerts a significant influence on ecosystem dynamics. In another study, Wallace et al. (1982) have shown that experimental reduction of the lotic insect fauna reduces the breakdown, utilization, and subsequent downstream transport of organic matter, indicating that consumers are important in regulating energy flow and nutrient cycling in stream ecosystems (see also Brock 1967; Elwood et al. 1983). Thus, physical retention and macroinvertebrate processing are important mechanisms, along with the microbial action mentioned earlier, for closing or tightening the recycling process in streams and preventing the rapid throughput of materials.

Together, the RCC and nutrient spiraling concepts point to a shift from the view of streams as discrete segments to one of a continuous, interacting set of biological and physical processes along the stream gradient (Newbold et al. 1982b; Cushing et al. 1983b). This shift should lead to a reevaluation of the idea that streams are conduits that simply transport materials from the land to the sea, and hence to a greater appreciation of the metabolic and retention roles streams play.

Recognition of the Importance of Biotic Interactions within the Stream Community

One of the underlying biases of research in lotic ecology has been that streams are highly variable and hence unpredictable. Consequently, stream communities often are regarded to be dominated by physical factors and highly individualistic (e.g. Winterbourn et al. 1981; Grossman et al. 1982). However, we suggest that while stream communities are not strictly deterministic, neither are they a hodge podge of organisms resulting solely from stochastic events (see e.g. Barnes and Minshall 1983). The probability theory of fluvial geomorphologists (Leopold and Langbein 1962), and the thermal equilibrium theory (Vannote 1978; Sweeney and Vannote 1978; Vannote and Sweeney 1980), clearly suggest that there is a high degree of predictability (and hence opportunity for determinism) embedded in the apparent stochasticity of streams. Also, as pointed out by Turelli (1981) and Schoener (1982), relatively small amounts of environmental fluctuation have small biological effects so that the simpler deterministic approach often is adequate. In addition, not only does the opportunity for density-dependent (deterministic) phenomena exist in streams (Horwitz 1978; Shiozawa 1983; Minshall et al. 1985) but, in fact, biotic determinants are operable (e.g. Hildebrand 1974; Hildrew and Townsend 1976; Bohle 1978; Peckarsky 1979, 1980, 1981; Peckarsky and Dodson 1980a, 1980b; Hart 1981, 1983; Wiley and Kohler 1981; Allan 1982; Fisher et al. 1982; Bruns and Minshall 1983; McAuliffe 1983, 1984).

The RCC is primarily a determimistic model to some (Winterbourn et al. 1981; Winterbourn 1982; Grossman et al. 1982); others view it as largely stochastic (Barmuta and Lake 1982; Fisher 1983). Actually it lies somewhere in between (see e.g. Levins and Lewontin 1980). For example, the RCC focuses on physical features of the environment as providing much of the habitat templet (sensu Southwood 1977) for stream communities, but it also is founded on trophic responses that are generally considered to be largely deterministic (Richardson 1980; Fisher 1983; Gorman and Karr 1978; Matthews 1982).

In addition to the relative spatial (longitudinal) and temporal predictability now believed to exist in stream environments, certain characteristics of the biota allow them to recover quickly from environmental fluctuations and thereby minimize the effects of what commonly are viewed as significant perturbations. In particular, the mobility, short life cycles, high reproductive rates, and ability to encyst or to burrow into the substratum allow stream organisms to avoid or adjust quickly to regular variations in the stream environment (e.g. flood resets) and to treat these variations essentially as *time constants* (see Hutchinson 1953) (e.g. Lehmkuhl and Anderson 1972; Minshall et al. 1985; Winget 1984). Studies of invertebrate colonization on introduced substrata (Minshall 1984) or following "catastrophic" flood and dewatering (Minshall et al. 1983a) also support the idea that rapid recovery from physical disturbance in streams is commonplace. Thus, these reset events are not really "stress," at the system level at least, and community structure is dependent on them in order to persist. Further, within the periods of physical variation (e.g. between spates) there commonly are sufficient time spans to permit the establishment and maintenance of equilibrium conditions. There seem to be certain periods during the year when equilibrium (hence deterministic or density dependent) conditions may prevail.

Most lotic consumers are trophic generalists or selective omnivores (Hutchinson 1981) that feed in proportion to the

broad kinds and amounts of foods available. Thus, the belief that competition for food is not a major factor in structuring stream communities is related to the widely held view that streams are highly variable and hence stochastic in nature. The RCC (and the data subsequently collected to test it: Hawkins and Sedell 1981; Minshall et al. 1982, 1983b; Cushing et al. 1983a) suggests that food relationships are important in structuring stream communities (see also Mackay and Wiggins 1978; Molles 1982). Lotic consumers also show morphological specialization with respect to food-gathering structures (Cummins and Klug 1979; Hale 1981; Merritt and Cummins 1978) resulting in considerable partitioning of food resources based on particle size, palatability, particle type, and constituents (Cummins 1973; Wallace et al. 1977; Anderson and Cummins 1979; Cummins and Klug 1979; Sheldon 1980; McAuliffe 1983). Ongoing competition for food has been demonstrated by Hart (1983) and McAuliffe (1983, 1984) whereas in other cases, resource partitioning (resulting in the "controlled" avoidance of competition) is evident (Minshall 1968; Mackay and Kalff 1969; Vannote 1978; Bruns and Minshall 1983).

Another important step in the development of stream ecosystem theory is the integration of certain principles of community ecology within the broader geomorphic/ecosystem context. The RCC, in conjunction with recent developments in population and community ecology (e.g. Cody and Diamond 1975; Southwood 1977; Anderson et al. 1979; Brown 1981; May 1981), suggests that the organization of lotic macroinvertebrate communities can be explained by the mean state of environmental variables and their degree of temporal variability and spatial heterogeneity. The gradient from headwaters to high-order reaches may be viewed as a spectrum of differentially variable habitats, and the patterns of species diversity for the total community and for specific functional groups appear to be interpretable within the context of habitat templets (see Southwood 1977). For example, we have found that components of community organization of lotic macroinvertebrates (e.g. species richness, niche breadth and overlap, and community complexity and stability) can be explained by the degree of temporal variability and spatial heterogeneity (D. A. Bruns, A. B. Hale, and G. W. Minshall, unpubl. data; Minshall et al. 1985). This structural approach complements previous RCC studies which emphasized ecosystem function. It also serves to introduce a conceptual basis for understanding lotic communities which in the past have been studied predominately from a descriptive aspect. And finally, it points the way for experimental investigations whereby mechanisms of community organization can be addressed directly.

Expansion of the River Continuum Concept to a Broader Geographic and Historical Model

The RCC defines a standard for natural, unperturbed lotic systems against which existing streams can be compared. The utility of the RCC lies in its identification of a set of general conditions and relationships that can be used to study and compare stream systems. In this context, the RCC provides a framework for understanding the ecology of streams and rivers and is not intended as a description of biological components of all rivers in the individualistic context (i.e. it is an abstraction in the sense of Levins and Lewontin 1980). The RCC defines a general condition and in so doing explains the interrelationships between sets of unique conditions. Regional and local deviations from the general pattern are a predictable result of specific variation in climate and geology, tributary influence, and location-specific lithology and geomorphology, as well as of long-term changes imposed by man. These factors are discussed more fully below.

Climate and Geology

Many geologists have accepted for sometime the idea that climate and geology are the ultimate determinants of river morphology through their effect on discharge and sediment load (e.g. Leopold and Wolman 1957; Gregory and Walling 1973; Lotspeich 1980). Together, climate and geology provide many factors influencing the characteristics of a river basin or watershed ecosystem. This has been accentuated by (1) the realization that river morphology and discharge can provide the templet for stream ecosystem structure and function (Curry 1972, 1976; Horwitz 1978; Vannote et al. 1980), (2) examination of stream ecosystem dynamics over different North American biomes (Minshall et al. 1983b), (3) efforts to classify watersheds as ecosystems (Warren 1979; Lotspeich 1980), and (4) attempts to evaluate streams outside the north-temperate region in a broader context (Winterbourn et al. 1981). Climate, of course, affects the type and density of vegetation (Kuchler 1964; Bailey 1978; Garrison et al. 1977) and the effect of climate on the stream is in turn intimately bound up with the pattern of vegetation (Ross 1963; Gregory and Walling 1973; Hynes 1975). For example, precipitation and vegetation interact to affect runoff and erosion and hence sediment yield and organic matter loading. In other words, the action of flowing water, and hence such things as bed form and stability and organic matter storage and transport, varies with climate (e.g. Peltier 1950; Gregory and Walling 1973; Minshall et al. 1983b).

Geology affects the relative erosiveness of the parent material in a drainage basin and, consequently, watershed topography, chemical load, bed composition, and the like. Geology gives each physiographic region its distinctive appearance. Within each region, geologic structure, acted on by processes controlled by climate, gives shape to each land form (Lotspeich 1980). Recently, Strayer (1983) has shown that stream size and surface geology are the major factors controlling mussel distribution in the streams of southeastern Michigan. Others (e.g. Minshall and Minshall 1978; Magdych 1984) have demonstrated how differences in water quality mitigated or caused by the underlying geology can profoundly affect major segments of the benthic invertebrate community. In fact, as noted by Magdych (1984), these findings suggest the need to modify the RCC to allow for multiple gradients if it is to be useful in the generation of ecological models in regions where abnormal (nongradient) chemical inputs are important.

The riparian system (Swanson et al. 1982) can override the effects of climate and geology to some extent, especially in small (first to fourth) order streams below the tree line. The riparian vegetation is seen as a "ribbon of continuity" that makes many headwater streams look very similar worldwide (Cummins et al. 1984). Within rather broad climatic limits undisturbed headwater streams have temporally stable accumulations of large woody debris. Also, there seem to be biochemical equivalents along these streams in terms of riparian plant inputs that show fast, intermediate, and slow rates of decomposition (K. W. Cummins, pers. obs.). Thus, shading, geomorphic structuring by woody debris, and biochemically analogous inputs from the riparian system result in similar functional group assemblages in spite of differences in geology and climate.

Further, it is evident that even in larger stretches of a river (greater than fourth-order) the floodplain or riparian zone cannot be uncoupled from the stream channel itself. The RCC (Vannote et al. 1980) stressed that the influence of the terrestrial system on a stream diminishes as the stream becomes larger and that autochthonous carbon inputs to higher order streams (seventh- to tenth-order) should increase while allochthonous inputs of carbon decrease. However, Sedell and Froggatt (1984) have shown that many rivers in pre- and early settlement times also were heavily subsidized by their local flood plains. This subsidy took several forms including local litter fall from extensive riparian forests and carbon inputs from sloughs and side channels. In addition, Triska (1984), in his review of the Red River, reported that between 1828 and 1876, woody debris from the riparian zone of this eighth-order stream was enough to cause log jams along a 400- to 500-km stretch of the river. Besides being a direct carbon input to the river, the logs acted as a physical retention device that caused flooding of the riparian zone, drowning of trees, and a further addition of material to the river.

Tributary and Related Influences

Tributary additions to master streams have a significant influence on the continuum pattern. Where tributary inputs deviate from their usual summative influence on river water quality, expected (sensu Vannote et al. 1980) trophic and community patterns may be altered. The magnitude of change depends on tributary size (Fig. 1), regional drainage density, vegetation cover, land use, and lotic versus lentic source of inputs. A variety of effects may be envisioned. Concentrations of nutrients and/or food items in the tributaries may be higher than in the mainstream and serve to increase the mainstream levels. This could lead to increases in algal production or filter feeder densities if limiting concentrations were exceeded. Alternatively, a tributary may serve to dilute the mainstream concentrations or to provide a sustained input of coarse materials to a mid- or high-order master channel which could result in a biotic structure and function similar to upstream reaches. These postulates have been substantiated by the studies of Bruns et al. (1984) in the Middle Fork of the Salmon River. Not only were tributary influences demonstrated but the differing effects of small and large tributaries were contrasted.

A corollary to the RCC has recently been developed which emphasizes the impact of man-made dams on stream dynamics (Hauer and Stanford 1982; Ward and Stanford 1983). Ward and Stanford (1983) visualized the effect of relatively high dams as producing a shift in stream ecosystem structure and function in either an upstream or downstream direction depending on the size of the stream on which the dam is located and the position of outflow relative to the thermocline. The expected effects are similar to those postulated for tributaries. Extensive pools, whether generated by dams or associated with low gradient (Brown and Brown 1984), appear to have predictable impacts on stream conditions which represent local modifications to the trend expected for rivers in general (Vannote et al. 1980; Magdych 1984).

Local Lithology and Geomorphology

Here the focus is on location-specific variations in local geology and in the morphology of the river channel (perhaps most evident in flow patterns and substratum composition). The classic view of a river system is one of progressive change from high-gradient, turbulent, rocky headwaters to low-gradient, sluggish, mudbottomed rivers, and with a channel pattern progressing from straight, through braided, to meandering. Further reflection indicates that the ideal rarely is so clearly achieved. For example, in the Salmon River the steep-gradient headwaters descend immediately to a low-gradient glacial valley, and channel pattern varies from straight to meandering to braided and back to meandering, then straight, then braided. In addition to differences in hydraulic dynamics associated with these changes, one may expect major shifts in such factors as riparian inputs, channel storage of organic matter, and interchange with the flood plain (Fig. 2).

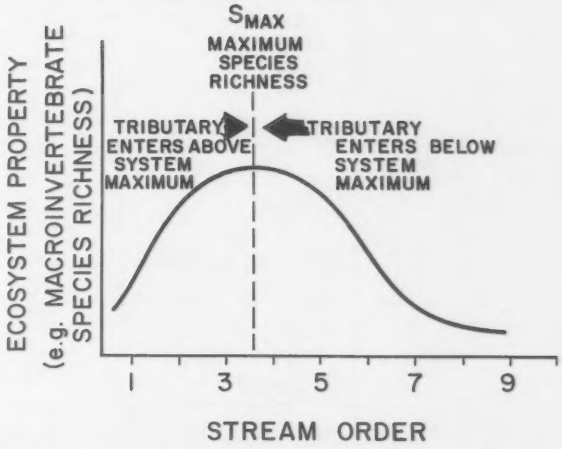


FIG. 1. The effect of a tributary on stream ecosystem parameters depends on where the tributary enters the larger stream. If a tributary enters above the point of system maximum it will drive the stream to that maximum. If it enters below it will move it back to reset that parameter. In this example, species richness reaches a maximum in third- to fourth-order streams. Tributaries entering above this cause the community to reach its maximum sooner. Tributaries entering below the peak increase richness by driving the system back.

Studies on the distribution of *Gonidea angulata* and *Margaritifera falcata* in relation to substrate and periodic temporal variations in runoff amply demonstrate the influence of local lithologic and geomorphic processes on the relative abundance and population size structure of these organisms (Vannote and Minshall 1982). *Gonidea angulata* was predominant and possessed high population densities on stabilized sand and gravel bars; *M. falcata* was predominant in cobble and boulder areas. On cobble areas unprotected by block boulders, most *Margaritifera* populations were relatively young (20–40 yr) and had an approximately normal size distribution. On boulder controlled substrates, the size frequency was skewed towards the larger, old (100 yr) age-classes. Periodic floods, perhaps approaching a 50- to 100-yr return period, apparently cause high mussel mortality by bed scour in most canyon habitats. This periodic scour keeps populations relatively young with an approximately normal size distribution. In contrast, where mussel beds are protected by a field of large block-boulders, the dissipation of kinetic energy during floods is primarily through turbulence within the water column rather than bed shear. In these rare but highly stable habitats, *M. falcata* attains maximal density, old age, and a population structure that is skewed towards large individuals. Thus, local (site specific) conditions may alter both community and population structure and con-

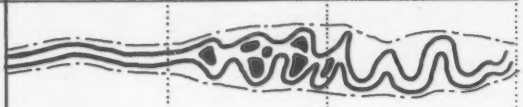
GEOMORPHIC FEATURES			
	CANYON	BRAIDED	MEANDERING
PARAMETER			
Stream Surface Area : Discharge	LOW	HIGH	MEDIUM
Riparian Inputs	LOW	HIGH	MEDIUM
Detrital Storage	LOW	HIGH	MEDIUM-HIGH
Area Flooded	SMALL	LARGE	MEDIUM

FIG. 2. Shifts in important ecosystem parameters in response to changes in geomorphic features resulting from differences in hydraulic dynamics at different points in a stream reach.

found efforts to obtain an accurate holistic view unless they are taken into account.

Long-Term Effects of Man

Townsend (1980) contended that the spatial aspect of streams can be viewed without regard to the temporal. However, recent research (Molles 1982; Cummins et al. 1983, 1984) suggests that both a spatial and a temporal scale must be employed to obtain an understanding of stream dynamics. This is particularly important, since our concept of aboriginal conditions presently is so poor (at least 100 yr of nonendemic, man-made effects in South America and Africa, up to 400 yr in North America, and 1000 yr or more in Europe).

The impact of man on the structure of ecological communities is a common theme running through modern environmental science and pollution biology. However, man's greater responsibility for wholesale alteration of communities and extinction of species over the entire historical record has only recently been suggested (Goudie 1981; Lewin 1984) and may be a much larger effect than thought. In stream research the intimate connection between the stream and the adjacent terrestrial environment has focused attention on how man-caused disturbances such as fire (Minshall et al. 1981), silviculture (Molles 1982), riparian control (Cummins et al. 1984; Sedell and Froggatt 1984), and tree debris removal (Triska 1984) have potential for long-term changes in stream systems. This awareness has been accentuated by the need for resource managers to know the natural, presettlement conditions of areas under their supervision (Romme 1982; Romme and Knight 1982; Sedell and Luchessa 1982). Various postsettlement alterations likely to have had major impacts on the nature of stream ecosystems include the following: urbanization; deforestation; tillage; irrigation; dam construction; channel alteration for navigation, logging, mining, and flood control; virtual extermination of beaver, bison, and other large mammals including aboriginal man; grazing by domestic animals; and fire suppression. These changes, many of them so subtle as to go unnoticed, have made it difficult for modern stream ecologists to place their findings in perspective with reference to natural, pristine conditions or to obtain meaningful measurements of certain aspects such as carbon budgets (Cummins et al. 1983). Nevertheless, incorporation of a broad temporal perspective has begun to aid substantially in the understanding of stream ecosystem structure and function both past and present (Molles 1982; Romme and Knight 1982; Sedell and Luchessa 1982; Sedell et al. 1982; Cummins et al. 1983; Fremling and Claflin 1984).

Side channels, braided channels, and off-channel backwaters (seasonal) may have an effect similar to that of tributaries. However, the massive snag removal that took place on essentially all North American rivers in the late 1800's and early 1900's, together with large-scale channelization efforts, has converted the majority of streams greater than fourth- to sixth-order from heavily braided or meandering systems to single, relatively straight channels (see e.g. Cummins et al. 1984; Fremling and Claflin 1984; Sedell and Froggatt 1984; Triska 1984). Thus, instead of a single fifth-order channel there might have been five third-order channels. Among other things, this would mean that the riparian effect was much different prior to such alterations. Wood, removed by man, probably produced a very different channel form in midsized rivers than that found today. Braids, off-channel backwaters, and side-channel streams probably caused many midorder rivers to behave more like headwaters. However, intensive beaver activity prior to the mid-1800's may have had a countereffect in that the extensive impoundments the beaver created would have made headwater streams wider, slower, and more midorder in character.

Implications to Stream Ecology

Deviations in regional and local conditions (associated with such things as climate and geology, tributaries and related

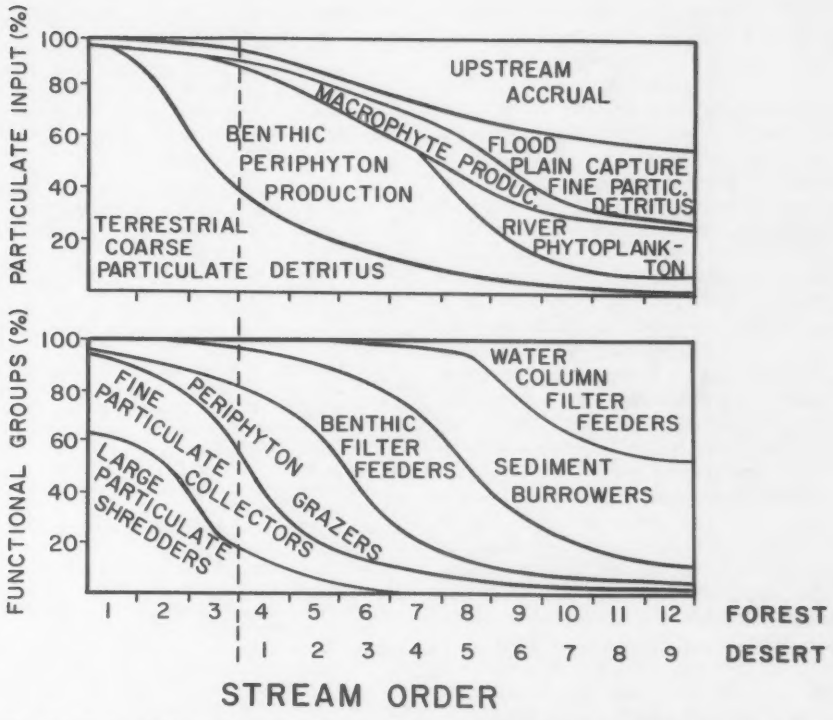


FIG. 3. Expected changes in particulate organic matter inputs and functional feeding group relationships along a river system (after Vannote et al. 1980). The abscissa is shown as a "sliding scale" to emphasize the fact that different streams enter the continuum at different points. In the two cases illustrated, forest streams begin with a strong terrestrial influence (reflected by a predominance of allochthonous organic matter and detrital processors) whereas desert streams, due to the lack of shading and reduced influx of allochthonous detritus, enter the sequence at a point displaced to the right and equivalent to a more downstream position of the forest stream.

influences, local lithology and geomorphology, and long-term effects of man) suggest that adjustments need to be made in the RCC if it is to be applied across biomes, especially when environmental extremes or unusual situations are involved. For example, in some wooded parts of Africa (e.g. Zimbabwe), large amounts of coarse particulate leaf detritus do not reach the stream. Most leaf material is processed by terrestrial detritivores during the dry season, and by the time the rains come, the coarse material has already been reduced to fine particles (R. C. Petersen, pers. obs.). Consequently, an important functional feeding group (shredders) is reduced or absent from such streams, and a sequence of adjustments in invertebrate trophic structure results (Fig. 3). The absence of large-particle shredders also appears to be typical of unstable, poorly retentive headwater streams in disturbed watersheds (Rounick and Winterbourn 1983a, 1983b). As another example, there are many areas of the world in which, for one reason or another, headwater streams (first-order woodland streams) simply do not occur. In areas dominated by porous calcareous geology such as in Florida (Odum 1957) or the western mountains of Jamaica (Petersen 1984; pers. obs.), the rivers begin as larger sized systems. In these rivers it still is expected that the basic sequential model will be followed but the river will skip the upper small-order categories and the effect that those small systems have on the downstream reaches will be removed. In Jamaican springs, which begin with a width of 30–40 m, the streams below the springs are dominated by primary production (macrophytes and periphytic algae). The grazer functional group, consisting of snails, dominates the macrobenthos, and due to a lack of particulate organics, filter feeders are rare but collector–gatherers feeding on decomposing macrophytes are abundant. In short, the system structure is similar to a midorder woodland river but without the filter feeders that normally feed on the upstream losses of particles. The need to accommodate these sorts of changes are explicit in the original formulation of the RCC (Cummins 1975; Minshall 1978; Vannote et al. 1980) but the point has been missed by some investigators (e.g. Winterbourn et al. 1981; Rounick and Winterbourn 1983a).

Because streams are ecosystems with numerous linkages and feedback loops, care must be taken in developing and testing stream ecosystem theory that critical interrelations are not excluded or unconsciously left uncoupled. For example, some investigations have taken the absence of macroinvertebrate shredders from certain headwater streams as failing to support the RCC (e.g. Winterbourn et al. 1981). But the various facets of organic matter processing cannot be viewed in isolation. For one thing, it is unreasonable to expect macroinvertebrate shredders to be present if the coarse particulate organic matter supply is inadequate or unreliable. Also, various trade-offs may occur in which the macroinvertebrate shredders may be replaced or supplemented by other size-reducing mechanisms (microbes, beaver, physical fragmentation). The important point in terms

of the RCC is that when coarse particulate organic matter enters a stream it will be reduced to fine particulate organic matter and that this phenomenon generally is quantitatively most significant in the headwaters of a river system. It is only when these features are shown to be unimportant or absent that this aspect of the RCC can be shown not to hold. Furthermore, abnormal (often anthropogenic) factors may obscure or obliterate the expected response such as when the entrance of geothermal waters or other adverse environmental conditions selectively eliminates certain components of the community. Sometimes such influences may occur on a large scale (e.g. acid rain), further obscuring the relationship and giving the impression that the general presettlement pattern is being examined. This is especially true if the event is a temporally distant one where the cause is separated from its present-day effect by time as well as space. Examples include acid rain in Europe which began with the Industrial Revolution and deforestation of large tracts of land which in parts of England may date back 3000 yr to the Bronze Age (Dr. W. Pennington, Botany Department, University of Leicester, U.K., pers. comm.).

Since stream ecosystem dynamics also are coupled closely to the fluvial geomorphic conditions, these conditions must be taken into account when testing the RCC or devising alternative explanations. This suggests that, in examining conditions along a river system, samples should be taken so that the mean or most characteristic geomorphic conditions in each stretch are represented. For example, collections of organisms taken only from riffles along the course of a river may provide an erroneous view of general patterns of distribution, since the characterizing geomorphic properties of the stream reach may be being overridden by the sampling procedure and a depositional rather than an erosional biota may actually be the appropriate representative. Here, too, the long-term temporal perspective is an important one. Due to flow regulation, many stream channels, particularly in lowland areas, are over- (e.g. due to channelization) or under-fit (e.g. due to sedimentation) or otherwise managed in ways that alter the natural conditions (e.g. weed cutting). While these represent deviations, the extent of which can be measured against the RCC, they do not provide evidence of conditions that invalidate the concept.

Conclusion

Stream ecosystem theory has seen a number of important advances, especially in the past decade. The RCC is consistent with these views and has served to synthesize most of them into a workable general hypothesis. Although the worldwide generality of the model remains to be further evaluated, it appears that most riverine ecosystems generally can be accommodated within the current conceptual framework. In this regard, it appears that even systems identified as "exceptions" (e.g. Winterbourn et al. 1981) represent no more than variations on a central theme (e.g. if coarse particulate organic matter is not there, neither will shredders or large-wood geomorphic control, etc.).

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BOOK REVIEWS/COMPTES RENDUS

Uncommon Sense. The Life and Thought of Ludwig von Bertalanffy, (1901–1972), Father of General Systems Theory. *Mark Davidson. J. P. Tarcher Inc., Los Angeles, CA. 1983. 247 p. $22.50 (Cdn), hardcover.*

Who was Ludwig von Bertalanffy? What is General Systems Theory? Fisheries biologists use the Bertalanffy growth equations, as in the 1957 classic *On the Dynamics of Exploited Fish Populations* by R. J. H. Beverton and S. J. Holt. But Bertalanffy's contribution to aquatic sciences reached far beyond his work in the theoretical biology of organisms. Through his writings on open systems, which are open to the import and export of material and energy, Bertalanffy helped to develop our present perspective of ecology and ecosystems. By way of expanding on the relevance of *Uncommon Sense*, we present several examples of Bertalanffy's perspective as it has been developed in fisheries and aquatic ecology.

Fisheries ecologist F. E. J. Fry of the University of Toronto and limnologist R. A. Vollenweider of the Canada Centre for Inland Waters recently spoke of the way in which their science since the 1930's related to the ideas of Ludwig von Bertalanffy. Fry's (1947) classic *Effects of the Environment on Animal Activity* is well known to physiological ecologists the world over. Fry felt that his personal perspective and practice of biology resembled those of Bertalanffy with respect to the concepts of hierarchical organization (form developing within form) in natural systems, of the role of form and structure in facilitating biological organization and self-regulation, and of the necessity for holistic study of integrated systems, to complement reductionistic study. Hence, Fry had an on-going interest in Bertalanffy's work, and had occasion to interact personally with Bertalanffy after World War II.

Vollenweider, recently appointed international co-president of the Alessandro Volta Centre for Advanced Environmental Studies in Como, Italy, described the development of limnology as a science in Europe during the 1930's and 1940's, and spoke of the "missing link" that the open-system perspective offered limnologists, who had been studying lakes as autonomous entities. The conceptual unification of the lake with its landscape was a novel scientific approach at that time, and facilitated the type of science developed in Vollenweider's "underground" classic *The Scientific Basis of Lake and Stream Eutrophication, with Particular Reference to Phosphorous and Nitrogen as Eutrophication Factors* (Vollenweider 1968), and in other whole-system perspectives of fisheries and aquatic ecology.

More recently, D. Pauly of Kiel University (and now at the International Centre for Living Aquatic Resources Management in Manila) studied Bertalanffy's work, which helped Pauly to develop some interesting and useful generalizations on the ecology of fish populations, for example as summarized in his "auximetric grid" (Pauly 1979).

One of us (H.A.R.) has been a rather casual student of Bertalanffy's work since an encounter with him in the early 1950's; the other (R.J.S.) was introduced more recently to Bertalanffy's ideas through references to open systems in geomorphological literature (i.e. Chorley 1962; Leopold and Langbein 1962) and in the River Continuum Concept of Vannote et al. (1980). We and others have recently been interested in ways that humans' intensely abusive practices regarding aquatic ecosystems cause reversals of some natural ecosystem tendencies, such as progressive centralization, differentiation, and integration. In this aspect, and as regards general systems approaches in general, we have found the book *Uncommon Sense* to be a useful supplement to the widely scattered literature by and about Bertalanffy.

Davidson's book is much more than a biography of Ludwig von Bertalanffy; only one chapter is devoted to the fascinating story of Bertalanffy's private life, including its disruption by World War II, and his subsequent appointments to universities in Austria, England, Canada, and the United States. Bertalanffy lives on in his ideas, and that is Davidson's focus.

The "Uncommon Sense" in the title of the book refers to General Systems Theory (GST), described by Bertalanffy 35 yr ago as "a new scientific doctrine, concerned with the principles which apply to systems in general" (Bertalanffy 1950). Bertalanffy originally called it *Allgemeine Systemlehre* or General Systems "Teaching" or "Doctrine," and he apparently felt that this conveyed more appropriately his notion of GST as a general *approach* to understanding the laws that govern the organization and interaction of systems. This relevant and far-reaching approach to scientific knowledge has found explicit or implicit application in many aspects of physics, biology, psychology, social sciences, and engineering — in many endeavours where complex phenomena are the object of study. The book discusses GST in all of these contexts, with some emphasis on the implications of GST in the design of social systems, and in the theory and practice of psychology as it relates to our perceptions of human nature. Of interest too is an account of developments complementary to GST, namely the various aspects of "systems technocracy," including systems engineering, operations research, linear programming, computer simulation, information theory, game theory, and cybernetics.

This well-written and nontechnical book should be rewarding reading for anyone interested in the origins and applications of GST. The reader will likely finish this book thinking that much of *Uncommon Sense* is now good common sense.

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Fish, pathogens and environment in European polyculture. Proceedings of an International Seminar, Szarvas, Hungary, 23–27 June 1981. Symposia Biologica Hungarica. Vol. 23. *Edited by J. Olah. Akademiai Kiado, Budapest. 1984. 265 p.*

This volume is composed of 24 papers presented at an International Seminar on Fish Health Problems held 23–27 June 1981 at Szarvas, Hungary. The stated purpose of the seminar was to bring together scientists to report research findings on important diseases of cultured freshwater pond fishes. Researchers came from the Federal Republic of Germany, the German Democratic Republic, Poland, Hungary, Bulgaria, Yugoslavia, Union of Soviet Socialist Republics (USSR), Czechoslovakia, Switzerland, and the United States. The inclusion of the United States seems a bit inconsistent because the theme was European polyculture.

Subject matter included viral diseases (4 papers), bacterial diseases (4 papers), parasites (9 papers), environmental effects (4 papers), and immunology (3 papers). The most important topic addressed was the etiology and description of gill necrosis (3 papers). This disease causes serious problems in European cultured carp. At present, it is not clear whether the cause is infectious or environmental, or both.

Presentations in all sections varied from the current status of various diseases to ongoing research on specific topics. This reviewer found several of the papers to be particularly informative: one dealt with the spread of *Bothriocephalus acheilognathi*, another on effects of environmental stresses on serum enzymes, and still others on histopathology and the viral nature of gill necrosis, and vaccination of fish in European pond culture.

Unfortunately, the awkward writing style of some papers made for difficult reading. Also, the reproduction of halftone figures left much to be desired. Generally speaking, the intent of the symposium was accomplished, and the interested reader can obtain a general understanding of the major diseases associated with European polyculture.

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Zooplankton of the Great Lakes: A Guide to the Identification and Ecology of the Common Crustacean Species. *Mary D. Balcer, Nancy L. Korda, and Stanley I. Dodson. University of Wisconsin Press, Madison, WI. 1984. xi + 174 p. $35.00 (U.S.)*

The St. Lawrence Great Lakes constitute the greatest accumulation of fresh water in the world, the study of which, after a very slow start, has blossomed in recent years. Several laboratories are devoted in whole or in part to investigations of these lakes, as well as to the training of students and school teachers.

As one might expect from the large size and varied environmental conditions in the lakes, the plankton communities are very complex. No publication has been available for the easy determination of zooplankton species, other than taxonomic works that include many species not occurring in the Great Lakes, making it hard for beginners who have limited taxonomic experience to ascertain the identity of their specimens.

The appearance of the present guide will be very welcome as a convenient aid in determining species of planktonic crustaceans. A similar companion manual on the determination of other zooplankters (especially rotifers) also would be useful.

Because it is designed primarily as a student laboratory manual, this guide begins with a discussion of the general morphology (external only) and ecology of the major taxa reported (Cladocera, Copepoda, Mysidacea, Isopoda, and Amphipoda). A list is given of 105 species (in some instances only genera) of crustaceans that have been reported from the Great Lakes plankton (many of them are tychopelagic and not truly holoplanktonic). A very usable key is presented for the determination of orders, families, genera, and species of the more commonly encountered forms. This is followed by discussions of the taxonomy, life history, and ecology of 26 of the most important species. A series of 41 plates, each with only one or two species illustrated in excellent large drawings, helps the student in identifying the various common species. Finally, there are brief descriptions of some of the less common taxa, a chronological summary of collections reported in the literature from each lake, a short glossary of technical terms, and a bibliography.

The manual, which is a sturdy ring-back production, seems very well printed, with few typographical errors. The necessity to summarize only very briefly the general characteristics of the several orders has resulted in a few questionable statements. For example (p. 7), the cladoceran ephippium is described as "thick and dark-colored, forming a saddlelike case ... around the eggs." This description is reasonably adequate for the genus *Daphnia*, but hardly for all cladocerans. Calanoid copepods (p. 8) are depicted as "primarily filter feeders ...." Recent work has shown that calanoids are not truly filter feeders, and

furthermore, a number of them are carnivores or omnivores, including *Epischura*, which occurs in the Great Lakes.

Despite such minor criticisms, however, the book will be of great value to everyone dealing with Great Lakes plankton. It is recommended that it be made available to all students and other workers, though for juvenile copepods and for species of certain genera (such as *Ceriodaphnia*, *Chydorus*, and *Pontoporeia*) other references will have to be consulted. Such references are mentioned in the text and detailed in the bibliography.

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Lake Sediments and Environmental History. *Edited by Elizabeth Y. Haworth and John W. G. Lund. University of Minnesota Press, Minneapolis, MN. 1984. xv + 410 p. $55 (U.S.).*

This compendium of 14 essays written by former students and colleagues of Dr. Winifred Tutin, FRS (nee Pennington), commemorates her retirement from the Freshwater Biological Association (FBA) and the University of Leicester, U.K. Of the first five chapters dealing broadly with lake sediment chemistry and methods of dating (radionuclides, ^{210}Pb, paleomagnetism), the contributions by Engstrom and Wright (Chapter 1) and Oldfield and Appleby (Chapter 3) stand out as particularly useful, well-written contributions, especially to students wishing to gain an appreciation of the difficulties of interpretation of chemical stratigraphy in lake sediment and to apply ^{210}Pb techniques to date recent sediment. The essay by Cranwell (Chapter 2) on organic geochemistry of triterpenes, though concisely presented and well written, will, I suspect, be appreciated by only a few readers who have a strong background in organic chemistry. Dr. Thompson's essay on paleomagnetism is a fitting testimony to the late John Mackereth's creative genius and nicely serves to summarize the global significance of his contribution to paleolimnology and more broadly to the field of geophysics. the remaining chapters of the book (Chapters 6–14) are devoted to the biological pursuits of paleoecology (palynology, diatomology, and post-glacial vegetational history), understandably skewed toward the botanical disciplines because of Dr. Tutin's many notable contributions to these fields. For the serious practitioner of paleolimnology and to beginning students as well, the contributions by Howarth (Chapter 6) and by Davis et al. (Chapter 10) are important essays. The former provides a graphic example of how the chronology of diatom microfossils and pollen from multiple cores, when supported by well-documented drainage basin history and extant phytoplankton records spanning four decades, can be integrated to reconstruct in remarkable detail the ontology of a lake and its drainage. The example used is in this case the well-studied Blelham Tarn in the English Lake District which has undergone various stages of anthropogenic-caused nutrient enrichment. Davis et al.'s essay on sediment focussing is very well written and nicely summarizes the inherent difficulties one may encounter when attempting to reconstruct lake and basin vegetational history from single or too few "deep basin" cores. Dr. Deevey's somewhat "off the wall" essay "Stress, Strain, and Stability in Lacustrine Ecosystems" (Chapter 8) will appeal more to the theoretical ecologist than the paleoecologist and, in my view, is not particularly germane to the central theme of the volume. This is also true for the essay by Anderson (Chapter 11) on soil development in Denmark which, from what I could discern, had little to do with lake ontology or basin vegetative succession. The book closes with two papers on Holocene vegetational succession in western Ireland and northwest Scotland by W. A. Watts and Hilary Birks, respectively. I found these essays very interesting and easy to read, and I suspect that both of these contributions will be of greater interest to European botanists and paleoecologists than to North American practitioners.

The book is well presented with few technical errors, excellent photographic reproductions, and clear graphic and tabular presentations. Dr. John Lund's personal recollections of Dr. Tutin's early research efforts at FBA and subsequent career development in many wide-ranging fields of paleoecology and botany serves its purpose well as preface to the volume by setting the stage for the essays that follow and by adding several touching personal notes about her life, which I am sure will be appreciated by all who had the opportunity to work with Dr. Tutin. How well I remember the "fireside" discussions with Dr. Tutin and the late John Mackereth about man's impact on the drainages of the north and south basins of Lake Windermere, and how each with strong will and determination approached the problem of interpretation from their respective disciplines. Fate was not to allow John Mackereth to witness the convergence of their ideas in the decade of the 1970's into a scientifically sound (and meaningful) interpretation of Lake Windermere ontology, and as I close my review of this commemorative volume dedicated to the research work of Dr. Winifred Tutin, FRS, I cannot help but feel that John Mackereth, too, would have applauded this contribution.

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Historical Whaling Records, Including the Proceedings of the International Workshop on Historical Whaling Records, Sharon, Massachusetts, September 12–16, 1977. *Edited by Michael Tillman and G. P. Donovan. International Whaling Commission (Special Issue 5), The Red House, Station Road, Histon, Cambridge CB4 4NP, United Kingdom. 1983. 269 p.*

"It is ironic that the very records that have been witness to the taking of thousands of whales may serve as an important source in the effort to save them from extinction." So writes Stuart Sherman in this volume, and his statement reveals the general thrust of the book.

By examining early logbooks of whaling vessels and private journals written during voyages through the world's oceans, cetacean biologists can extend the relatively continuous and reliable records compiled during twentieth century factory ship

whaling back into the era of sail whalers and hand-thrown harpoons. The slow population growth of species of great whales makes a long continuum of catch data necessary for the design of effective management policies today. Tillman explains that the purpose of the original workshop was "to determine if the study of early whaling records could be a viable approach to the problem of estimating initial abundance of whale stocks and of determining the effect of exploitation upon them." As the body responsible for regulation of the world's whaling industry, the International Whaling Commission (IWC), one of the sponsors of the Sharon workshop, undertook the publication of these proceedings.

Thirty-five sorts of historical whaling records were described by Sherman (1965) in *The Voice of the Whaleman*. Of these, logbooks and journals have been most often used by historians, geographers, anthropologists, economists, oceanographers, glaciologists, and botanists, because they provide details about events on the whaling grounds and at ports visited during the voyage. With the notable exception of Townsend (1935), who mapped more than 53 000 kills of four whale species from logbook data, zoologists have generally made little use of such documents until recently. One can only speculate on the reasons: less urgency perceived a few decades ago concerning the plight of the great whales; a lower priority assigned historically to cetacean biology; skepticism about the potential usefulness of historical sources (which one of the book's editors admits to, before he "saw the light" during the Sharon workshop); insufficient time, patience, or motivation to locate and study widely scattered manuscript documents; or conceivably a feeling that Townsend had exhausted the possibilities of such material.

Whatever the reasons, after a half-century of neglect, historical whaling records are again acceptable — even desirable — to biologists. The book effectively demonstrates that information Townsend probably never dreamed of is now being coaxed out of the "old, musty whaling logbooks and journals" of which Tillman was once skeptical — things such as stock identity, initial population size, population trends during exploitation, catch per unit effort, migration routes and dates, and some aspects of whale behaviour.

One of the contributors, George Shuster, suggests, for a first priority in sperm whale research from historical records, locating Townsend's original notes, which under modern methods of analysis might provide valuable unpublished baseline information with which more recent facts could be compared. It is therefore of great interest to find that one of the happy outcomes of the Sharon workshop was in fact the discovery by the New York Zoological Society of the original data extracted by Townsend in the 1930's, lying abandoned in a tunnel at the New York Aquarium, "water damaged and fragile." It is now being restored.

The book contains 17 papers by 19 authors from six countries (Australia, Canada, England, Japan, South Africa, United States). Most of the contributors are biologists but historians, librarians, museum curators, and archeologists are represented too. Approximately half the papers are case studies based at least in part on whaling logbooks and journals, or on other whaling records such as annual tabulations of voyages and catch. The case studies deal either with particular species (including sperm whales, Greenland or bowhead whales, and humpback whales) or particular regions (such as the waters surrounding the Galapagos Islands, the western Pacific Ocean, and the western Indian Ocean). Other papers discuss the nature and limitations of historical whaling records, their potential use, data extraction and storage, methods of estimating initial stock sizes, and other important topics. The combination of case studies and theoretical papers is a useful one and should broaden the appeal of the work.

Altogether, the hard-covered volume amounts to 269 pages. Its cover is enlivened with an artist's rendition of a nineteenth century arctic scene, and inside there is a generous assortment of illustrations ranging from photographs and sketches of whaling operations to maps, graphs, and other diagrams. In format the individual papers resemble contributions to the IWC annual report series, neatly compartmentalized under headings and subheadings, and accompanied by lengthy tables, lists of references, and sometimes appendices. The standardization breaks down in the matter of abstracts — only seven papers have them. In the list of contents the papers do not masquerade as chapters. They are clearly IWC reports, each identified (unnecessarily I think) with the mysterious codes normally assigned to units in the annual reports. (One is called SC/Jn80/SpW18; another is HWR/6 + 7.) There is no list of figures, no index, and no information on how to order the book or how much it costs. Thus, the volume makes no pretensions to being an appealing, coherent book, attractive and available to general readers. It is a collection of scholarly papers and it will be of interest mainly to those involved in whaling research or the preservation and organization of historical whaling records. Nonetheless there is a deal of interesting whaling history within the case studies of regions and species, from new points of view.

Considering the international distribution of the contributors and the vast number of figures, tables, and references, Tillman and Donovan (themselves separated by 5000 miles) have accomplished a formidable task in preparing these papers for publication in one volume. Six years does seem an unnecessarily long time to wait for publication of conference proceedings, however! A lot of water has flowed under the flukes in the meantime. Nonetheless, because this collection of papers emphasises the reconstruction of whale characteristics from historical records, it constitutes a unique contribution to the literature of whaling and scientific method.

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(R615)

BOOKS RECEIVED/LIVRES REÇUS

The mangrove ecosystem: research methods. *Edited by S. C. Snedaker and J. G. Snedaker. United Nationals Educational, Scientific and Cultural Organization, 7 place de Fontenoy, 75700 Paris. 1984. xv + 251p. ISBN 92-3-102181-8.* This monograph provides a general understanding of the mangrove ecosystem and represents a consensus of scientific opinion on the relevant directions for new research. [R636]

Rare, endangered and extinct fishes in Canada. *Don E. McAllister, Brad J. Parker, and Paul M. McKee. Syllogeus 54. National Museums of Canada, National Museum of Natural Sciences, Ottawa, Ont., Canada. 1985. 192 p. ISSN 0704-576X.* A review of the overall status of Canada's freshwater and marine fish faunas with a general discussion of problems affecting the environment. [R637]

La pêche et les pêcheurs des provinces maritimes du Canada. *Jean Chaussade. Les Presses de l'Université de Montréal, Montréal (Qué.). 1983. 302 p. $28.00. ISBN 2-7606-0585-X.* Contribution à l'étude du sous-developpement à l'intérieur d'un pays riche; une forme raccourcie d'une thèse de doctorat d'État soutenue en 1980 à l'Université de Bretagne Occidentale (Brest). Il s'agit d'une étude de géographie humaine. [R638]

Biologia Acuatica No. 6. Bibliografia Limnologica Argentina 1979–1983. *Compiled by J. P. Gomez, L. C. Protogino, J. M. Iwaszkiw, H. L. Lopez, N. A. Bo, C. A. Darrieu, M. M. Martinez, and L. A. Spaletti. Instituto de Limnologia "Dr. Raul A. Ringuelet", Casilla de Correo 55, (1923) Berisso, Argentina. 1984. 55 p. $10.00 (U.S.) (includes postage). ISSN 0326-1638.* A listing of 616 titles on works related to the limnology of Argentina. [R639]

Pêche, biologie et dynamique du tassergal (*Pomatomus saltator*, Linnaeus, 1766) sur les côtes sénégalo-mauritaniennes. *Travaux et documents de l'ORSTOM 168. Service des Publications de ORSTOM Bondy (France). 1983. 279 p. ISBN 2-7099-0711-9.* La majeure partie du livre a été rédigé par Monsieur C. Champagnat. Après son décès ses collèagues ont terminé le manuscrit se servant de ses notes et l'ont publié à mémoire. [R640]

Labor developments in the fishing industry. *Edited by Jean-Louis Chaumel. Canadian Special Publication of Fisheries and Aquatic Sciences 72. 1984. 90 p. $6.00 (Canada), $7.20 (other countries). ISSN 0706-6481, ISBN 0-660-11746-0. Proceedings of an international symposium held at Rimouski, Quebec, November 3 and 4, 1983.* A report on working conditions for fishermen and processing plant workers and aspects of technological changes and productivity with a discussion of conditions governing the survival of coastal communities. [R641]

Évolution des milieux de travail dans le secteur des pêches. *Rédacteur Jean Louis Chaumel. Publication spécial canadienne des sciences halieutiques et aquatiques 72. 1984. 90 p. 6 $ (Canada), 7.20 $ (autres pays). ISSN 0706-6481, ISBN 0-660-91398-4. Actes du colloque international tenu à Rimouski (Québec) les 3 et 4 novembre 1983.* Un rapport sur l'état des conditions de travail pour les pêcheurs et travailleurs d'usine et les aspects relatifs aux changements technologiques et à la productivité avec un discussion des conditions de survie des communautés côtières. [R642]

Contaminant effects on fisheries. *Edited by Victor W. Cairns, Peter V. Hodson and Jerome O. Nriagu. Volume 16 of Wiley Series in Advances in Environmental Science and Technology. John Wiley & Sons, Inc., New York, NY. 1984. 333 p. $69.96 (U.S.). ISBN 0471-88014-0.* Leading toxicologists and fisheries biologists from Canada and the United States examine the bioaccumulation, metabolism, metabolism, and excretion of toxicants by fish. Special attention is paid to epidemiology of fish diseases induced by toxicants and to strategies for reestablishing disturbed fisheries. [R643]

Proceedings of the national aquaculture conference. *Strategies for aquaculture development in Canada. Edited by G. I. Pritchard. Canadian Special Publication of Fisheries and Aquatic Sciences 75. 1984. 131 p. $8.00 (Canada), $9.60 (other countries). ISSN 0706-6481, ISBN 0-660-11745-2.* The conference held at St. Andrews, New Brunswick July 10–14, 1983, was a timely review of the status of aquaculture in seeking alternative and more intensive production systems for finfish, shellfish, crustaceans, and marine plants. The papers are of Canadian origin in order to obtain an accurate reflection of Canadian industry and its opportunities. [R644]

Comptes rendus de la conférence nationale d'aquiculture. *Mesures pour le développement de l'aquiculture au Canada. Rédacteur G. I. Pritchard. Publication spéciale canadienne des sciences halieutiques et aquatiques 75. 1984. 142 p. 8 $ (Canada), 9.60 $ (autres pays). ISSN 0706-649X, ISBN 0-660-91397-6.* La conférence qui a eu lieu à St. Andrews (Nouveau Brunswick) du 10 au 14 juillet 1983 a permis de faire, en temps opportun un examen de l'état de l'aquiculture dans sa recherche de nouveaux systèmes plus intensifs pour la production de poissons, de mollusques, de crustacés et de plantes marines. Ces documents sont d'origine canadienne afin de

se conformer au désir d'obtenir une image précis de l'industrie canadienne et de ses possibilités. [R645]

Olympic wild fish conference proceedings. *Edited by J. M. Walton and D. B. Houston. Available from James M. Walton, Peninsula College Fisheries, 1502 East Lauridsen Boulevard, Port Angeles, WA. 98362. 1984. 300 p. $15.00 (U.S.).* The proceedings of a 1983 conference with discussions on concerns about wild salmon, steelhead, cutthroat, and rainbow stocks in the Pacific Northwest. Contributions include results of significant research and management strategies. [R646]

Penaeid shrimps — their biology and management. *Edited by John A. Gulland and Brian J. Rothschild. Fishing News Books Ltd., Farnham, Surrey, England. 1984. 312 p. £30.00. ISBN 0-85238-131-X.* Selected papers from a workshop held in Key West, Florida, November 1981. Overview papers describe the shrimp fisheries of various countries, and their major problems. Other papers deal with specific aspects of shrimp biology and management. [R647]

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Le Symposium, parrainé par le ministère des Pêches et des Océans et organisé par la Direction de la recherches sur les pêches, consistera en 25 à 30 présentations dont la plupart seront des exposés de conférenciers invités. Les sujets traités comprendront :

- Les stratégies du cycle vital
- L'habitat et la production
- La gestion : passée, présente et future

Les personnes qui désirent obtenir de plus amples informations ou participer au symposium doivent s'adresser à M. Howard D. Smith, président, Sockeye '85, Station de biologie du Pacifique, Nanaïmo (C.-B.) V9R 5K6. Téléphone : (604) 666-6560.

CCFFR–CCRP

Ottawa, 6–7 January 1986

Preliminary Program and Call for Papers

Two invited paper sessions are planned for 1986. The first, scheduled for Monday morning, is entitled "Habitat selection and its relation to fisheries" and will be convened by D. L. Kramer. The second, scheduled for Tuesday, is entitled "Quantitative genetics and its application to aquaculture and fisheries" and will be convened by J. D. McPhail. The Stevenson Lecture will be presented on January 6.

Contributed papers sessions are planned for both afternoons. ***This is a call for abstracts.*** Type your abstract (maximum 200 words, single-spaced). Contributed papers will be selected by a committee of four; duration should be 15 minutes for discussion. Standard audiovisual equipment (35 mm and overhead projectors) will be available. We also plan to present posters; please indicate whether your paper should be considered as a poster or *could* be considered as a poster. Deadline for abstracts is August 30, 1985, and they should be sent to Dr. D. L. Kramer, Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Que. H3A 1B1.

CCFFR–CCRP

Ottawa, les 6 et 7 janvier 1986

Programme préliminaire et demande de résumés

Deux séances avec des conférenciers invités sont au programme pour 1986. La première, prévue pour le lundi matin, s'intitule « La sélection de l'habitat et sa relation avec les pêcheurs ». Elle sera animée par D. L. Kramer. La seconde, prévue pour mardi, s'intitule « La génétique quantitative et son application à l'aquiculture et aux pêches ». Elle sera animée par J. D. McPhail. La conférence à la mémoire de J. C. Stevenson aura lieu le 6 janvier.

Une séance de présentation de documents est prévue pour les deux après-midi. ***Nous vous invitons par la présente à envoyer vos résumés.*** Le résumé doit être dactylographié (200 mots au maximum, simple interligne). Les résumés présentés seront évalués par un comité de quatre personnes. Quinze minutes seront allouées à la discussion. Des appareils audio-visuels (projecteur 35 mm et rétroprojecteur) seront à votre disposition. Nous avons aussi l'intention de présenter des affiches ; veuillez indiquer si votre résumé devrait ou *pourrait* être affiché. La date limite d'envoi des résumés a été fixée au 30 août 1985. Veuillez le faire parvenir à Dr D. L. Kramer, Département de biologie, Université McGill, 1205, avenue Docteur Penfield, Montréal (Qué.) H3A 1B1.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Are age-structured models appropriate for catch-effort data? **D. Ludwig and C. J. Walters**

Yolk absorption, yolk sac constrictions, mortality, and growth during first feeding of Atlantic salmon (*Salmo salar*) incubated on astro-turf **T. J. Hansen and D. Møller**

Factors affecting variability of trapnet catches **J. M. Hamley and T. P. Howley**

Responses of *Isonychia bicolor* to alkaline pH: an evaluation of survival, oxygen consumption, and chloride cell ultrastructure **G. T. Peters, D. S. Cherry, and J. Cairns, Jr.**

Relationship of crayfish (*Orconectes virilis*) growth to population abundance and system productivity in small oligotrophic lakes in the Experimental Lakes Area, northwestern Ontario **R. L. France**

Chemistry of Lake Hovvatn, Norway, following liming and reacidification **R. F. Wright**

Planktivory in a littoral-dwelling lake fish association: prey selection and seasonality **A. Keast**

Effective solvents and extraction periods employed in phytoplankton carotenoid and chlorophyll determinations **N. D. Bowles, H. W. Paerl, and J. Tucker**

The influence of fish–zooplankton–phytoplankton interactions on the results of selenium toxicity experiments within large enclosures **A. Salki, M. Turner, K. Patalas, J. Rudd, and D. Findlay**

Biology of the bathylagid fish, *Leuroglossus schmidti*, in the Strait of Georgia, British Columbia, Canada **J. C. Mason and A. C. Phillips**

Recent changes in the inshore forage fish of Lake Michigan **D. J. Jude and F. J. Tesar**

Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed **M. Fréchette and E. Bourget**

Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer **M. Fréchette and E. Bourget**

Organic nitrogen compounds in atmospheric precipitation: their chemistry and availability to phytoplankton **M. H. Timperley, R. J. Vigor-Brown, M. Kawashima, and M. Ishigami**

Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens* **L. G. Rudstam and J. J. Magnuson**

The distribution and abundance of seals in the high Arctic, 1980–82 **M. C. S. Kingsley, I. Stirling, and W. Calvert**

Fish production in warmwater streams in Poland and Ontario **R. Mahon and E. K. Balon**

Notes

Phytoplankton response to freshwater runoff: the diversion of the Eastmain River, James Bay **R. G. Ingram, L. Legendre, Y. Simard, and S. Lepage**

The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams **C. J. Cederholm and N. P. Peterson**

Letters and comments/Lettres et commentaires

Comment **P. V. Hodson**

Reply **M. Gilbertson**

Book reviews/Comptes rendus

Toxic contaminants in the Great Lakes. Vol. 14 (edited by J. O. Nriagu and M. S. Simmons) **J. P. Geisy**

Methods in marine zooplankton ecology (M. Omori and T. Ikeda) **D. L. Mackas**

Announcements/Avis

Canadian Special Publication of Fisheries and Aquatic Sciences 75

Proceedings of the National Aquaculture Conference

Strategies for Aquaculture Development in Canada

Edited by
G. I. Pritchard

This publication contains the proceedings of the National Aquaculture Conference held at St. Andrews, New Brunswick, July 10–14, 1983, under the joint sponsorship of the Department of Fisheries and Oceans and the Science Council of Canada. It provided a timely review of the status of aquaculture in seeking alternative and more intensive production systems for finfish, shellfish, crustaceans, and marine plants. Readers will find a wealth of information in these papers, and unique aspects of aquaculture in Canada will be more readily apparent.

131 pages

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Publication spéciale canadienne des sciences halieutiques et aquatiques 75

Comptes rendus de la Conférence nationale d'aquiculture

Mesures pour le développement de l'aquiculture au Canada

Rédaction :
G. I. Pritchard

La présente publication contient les comptes rendus de la Conférence nationale d'aquiculture tenue à St. Andrews (Nouveau-Brunswick) du 10 au 14 juillet 1983 sous l'égide du ministère des Pêches et des Océans et du Conseil des sciences du Canada. La Conférence a donc permis de faire, en temps opportun, un examen de l'état de aquiculture dans sa recherche de nouveaux systèmes plus intensifs pour la production de poisson, de mollusques, de crustacés et de plantes marines. Le lecteur pourra trouver une masse importante d'informations dans ces documents qui rendent plus visibles les aspects uniques de l'aquiculture au Canada.

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Book reviews/Comptes rendus

Uncommon sense. The life and thought of Ludwig von Bertalanffy (1901–1972), father of General Systems Theory (Mark Davidson)	R. J. Steedman and H. A. Regier	**1056–1057**
Fish, pathogens and environment in European polyculture. Proceedings of an International Seminar, Szarvas, Hungary, 23–27 June 1981. Symposia Biologica Hungarica. Vol. 23 (edited by J. Olah)	G. L. Bullock	**1057**
Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species (Mary D. Balcer, Nancy L. Korda, and Stanley I. Dodson)	C. C. Davis	**1057–1058**
Lake sediments and environmental history (edited by Elizabeth Y. Haworth and John W. G. Lund)	J. G. Stockner	**1058**
Historical whaling records, including the Proceedings of the International Workshop on Historical Whaling Records, Sharon, Massachusetts, September 12–26, 1977 (edited by Michael Tillman and Gregory P. Donovan)	W. G. Ross	**1058–1059**

Books received/Livres reçus	**1060–1061**
Announcements/Avis	**1062**
Coming next month/À paraître le mois prochain	**1063**

Canadian Special Publication of Fisheries and Aquatic Sciences 73

Directory of Marine and Freshwater Scientists in Canada — 1984

The **Directory of Marine and Freshwater Scientists in Canada — 1984** is an inventory of marine and freshwater scientists and engineers in governmental organizations, universities, and industry who are engaged primarily in research and development, and consulting. The Directory also includes scientists engaged in scientific services and management.

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Publication spéciale canadienne des sciences halieutiques et aquatiques 73

Répertoire des experts des sciences de la mer et des eaux douces au Canada — 1984

Le **Répertoire des experts des sciences de la mer et des eaux douces au Canada — 1984** constitue une liste des ingénieurs et spécialistes des sciences de la mer et des eaux douces, membres des organismes gouvernementaux, des universités et de l'industrie, et dont les activités sont surtout orientées vers la recherche, le développement et les services de consultation. On y trouve aussi le nom d'experts en gestion et en services scientifiques.

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Section 4 Experts, domaines et activités
Section 5 Domaines et leurs experts

Les renseignements figurant dans le répertoire, qui exposent la situation de chaque scientifique en décembre 1983, ont été fournis par divers organismes à la demande du Comité canadien d'océanographie. Le répertoire est publié par la Direction de l'information et des publications scientifiques du ministère des Pêches et des Océans.

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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 42, No. 5, May 1985

Volume 42, nº 5, mai 1985

Articles

The utility of light-saturation models for estimating marine primary productivity in the field: a comparison with conventional "simulated" in situ methods W. G. Harrison, T. Platt, and M. R. Lewis **864–872**

Use of pup counts in indexing population changes in pinnipeds J. M. Berkson and D. P. DeMaster **873–879**

Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine – Scotian Shelf area in relation to oceanographic features M. Sinclair and T. D. Iles **880–887**

Stock assessment problems in Atlantic herring (*Clupea harengus*) in the northwest Atlantic M. Sinclair, V. C. Anthony, T. D. Iles, and R. N. O'Boyle **888–898**

Estuarine growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure J. D. Neilson, G. H. Geen, and D. Bottom **899–908**

An evaluation by field experiments of the McLay model of stream drift P. A. Larkin and D. W. McKone **909–918**

Movements of adult female Dungeness crabs (*Cancer magister*) in northern California based on tag recoveries N. Diamond and D. G. Hankin **919–926**

Model of sulphate concentration in a small stream in the Harp Lake catchment, Ontario H. M. Seip, R. Seip, P. J. Dillon, and E. de Grosbois **927–937**

Internal zonations in sections of vertebrae from Atlantic bluefin tuna, *Thunnus thynnus*, and their potential use in age determination E. D. Prince, D. W. Lee, and J. C. Javech **938–946**

Modeling the lethal effects of high temperature on fish D. M. Kilgour, R. W. McCauley, and W. Kwain **947–951**

A bioeconomic analysis of sequential fisheries: competition, coexistence, and optimal harvest allocation between inshore and offshore fleets A. T. Charles and W. J. Reed **952–962**

Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic J. G. Casey, H. L. Pratt, Jr., and C. E. Stillwell **963–975**

Predicting inshore whale abundance — whales and capelin off the Newfoundland coast H. Whitehead and J. E. Carscadden **976–981**

Comparison of constant effort harvest policies for fish stocks with variable recruitment J. E. Hightower and G. D. Grossman **982–988**

Interaction between stock area, stock abundance, and catchability coefficient G. H. Winters and J. P. Wheeler **989–998**

Responses of sea-ice microalgae to climatic and fortnightly tidal energy inputs (Manitounuk Sound, Hudson Bay) M. Gosselin, L. Legendre, S. Demers, and R. G. Ingram **999–1006**

Effects of dietary carbohydrate and water temperature on the chronic toxicity of waterborne copper to rainbow trout (*Salmo gairdneri*) D. G. Dixon and J. W. Hilton **1007–1013**

Reviews/Synthèses

Microstructure of fish otoliths S. E. Campana and J. D. Neilson **1014–1032**

Notes

Evidence of decreasing spatial diversity in British Columbia salmon stocks C. J. Walters and P. Cahoon **1033–1037**

Perspectives

Questions and comments on the River Continuum Concept B. Statzner and B. Higler **1038–1044**

Developments in stream ecosystem theory G. W. Minshall, K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote **1045–1055**

(*continued inside back*)

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